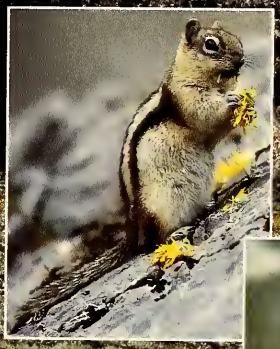
The Wild Mammals of Montana

by Kerry R. Foresman



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by
Kerry R. Foresman

Pen and ink illustrations by
Rexford L. McGraw, III

Photographs by Milo Burcham and the author

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I would like to dedicate this work to my parents, Kenneth and Louise Foresman, who encouraged me to pursue my goals throughout my life, whatever they might be. They were the first to introduce me to the wonders of the woods and I am forever grateful.

A special dedication, in memoriam, goes to Dr. Philip L. Wright, mammalogist and ornithologist, teacher and friend, who lit the spark in me to the field of mammalogy. "P.L." taught me mammalogy, as he did thousands of other students, during his 46 years at the University of Montana. His stories will surely be missed but not forgotten.

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Front Cover Photographs:
Golden-mantled ground squirrel, Bighorn sheep, and Grizzly bear with cub: Milo Burcham
American marten: Kerry R. Foresman
Background scene: Sagebrush plateau near Vipond Park, Beaverhead County: Kerry R. Foresman

Back Cover Photographs:
Vagrant shrew and Pika: Milo Burcham
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The pen and ink drawings by Rex L. McGraw, III throughout this text I think finely illustrate my points and it is hoped will make this information that much more useful.

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Dean E. Pearson—Color photograph: Plate 6, Fig. 3; Species accounts: *Synaptomys borealis.*

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Introduction

This book is intended to be used by everyone who enjoys Montana's outdoors whether for family outings, hunting trips, or professional activities of the forester, range manager, or wildlife biologist. Every effort has been made to keep this material "user friendly" and yet provide a more detailed and scientific approach to the subject than is currently available. Toward this end even the size and format of the text was considered, the intention being to provide a guide that can be thrown into one's day pack so that it is always readily available in the field.

The 1st chapter, entitled *Mammalian Characteristics,* is included to provide the reader with a clear understanding of the physical characteristics of this broad animal group, the mammals, and how these attributes have contributed to the evolution of the group as a whole. Immediately following is a chapter on the physical attributes of the state of Montana, *Physiography of Montana,* which addresses such topics as climate, topography, and habitat, qualities that clearly determine presence or absence of the species at hand. The true focus of this book, of course, is the 108 species of mammal found in the state. For each, a discussion is provided on taxonomic derivation, life-history traits, distinguishing characteristics, distribution in the state and throughout North America, general ecology, reproductive activities, current known status in the state, and requisite habitat associations.

Toward these goals the following approach has been taken to summarize our current knowledge. The taxonomic classification scheme proposed by Jones et al. (1997) in their *Revised Checklist of North American Mammals North of Mexico, 1997* has been adopted for this text unless otherwise noted. This taxonomic listing, updated roughly every 3 to 5 years, provides the most current and accepted rendition of North American mammalian systematics available. In addition, a recent article summarizing systematics of the mustelid–skunk families has been adopted (Dragoo and Honeycutt 1997). The reader must realize that taxonomy, by its very nature, is a dynamic scientific discipline. Our understanding of the relationship between 1 species and another, at every taxonomic level, can, and has, change(d) as we broaden our studies and apply ever more sophisticated methods to their analysis. The material presented herein is hopefully an accurate representation of the current state of our knowledge in this respect.

Following the introductory material for each taxonomic order, representative line drawings are provided to illustrate diagnostic skull characteristics. Additional line drawings illustrate diagnostic skull characteristics for each taxonomic family. For a detailed, illustrative key for the identification of all Montana species the reader should refer to the companion text, *Key to the Mammals of Montana* (Foresman 2001).

Each species account begins with a description of how, and by whom, the species was first described by the scientific community. Following this, the derivation of the scientific nomenclature applied to the species is provided, information determined in large part through the use of Jaeger's (1959) text, *A Source-Book of Biological Names and Terms.* Subsequent species accounts contain information on ecology and behavior, reproductive cycles, and current status in Montana. Extensive use has been made of *Mammalian Species* accounts, and literature cited therein, published by the American Society of Mammalogists although additional references are included, particularly those pertaining to Montana research or more recent information. Readers are encouraged to review these species accounts for more detail. Included as a supplement to the species accounts are high-quality col-

or plates for many of the 108 species, chosen not only for their ability to illustrate key characteristics, but hopefully to display the unique beauty of each species.

Montana distribution maps for each species have been updated based upon the author's (and his graduate students') work in the field over the past many years, and the work of other professional biologists both from within Montana and out of state. This information details the occurrence of each species on a county-by-county basis, information that reflects actual museum collection records, harvest records in the case of game species, or verified sightings by professional biologists. Distribution maps, by their very nature, are problematic. Their accuracy reflects collection efforts so gaps are not uncommon. Rather than simply "fill in the gaps" where the likelihood of occurrence is high, but for which no verification exists, I have chosen to designate such counties as probable occurrence. Thus, counties which are darkened reflect those in which specimens have actually been collected or recorded. Those that are lightly shaded reflect the probable occurrence of the species based upon broader, generalized North American range distributions described by other authors (Hall 1981; Hoffmann and Pattie 1968; van Zyll de Jong 1983), and habitat availability. In some instances, for example the lynx (*Lynx canadensis*), grizzly bear (*Ursus arctos*), and swift fox (*Vulpes velox*), the distribution presented reflects some historical museum records; disappearance of such species from some portions of the range described is highly likely. Given this approach, I hope to stimulate additional collection or sighting efforts which will provide verification of occurrence in counties now listed as probable and evidence for disappearance from previously occupied counties. All attempts have been made to identify and incorporate any substantive Montana materials held within museums in the United States. The holdings of the National Museum of Natural History at the Smithsonian Institution, Washington, D.C., the Museum of Natural History at the University of Kansas, Lawrence, the Museum of Zoology at the University of Michigan, Ann Arbor, the Bell Museum of Natural History at the University of Minnesota and obviously the museums of The University of Montana, Missoula, and Montana State University, Bozeman, have been particularly beneficial. Museum records, the author's private collections, and records from research in which animals were captured, identified, and released now number over 25,000. Additional distribution data also have been included from Montana Department of Fish, Wildlife & Parks records for game species hunted or trapped. Continuing discussions with professional field biologists working throughout the state have been included in this database. Within each species account the habitat to which each is associated is provided in as much detail as our current knowledge allows. This information, coupled with the discussion of habitat categories in the chapter on physiography, will allow the reader to determine whether or not a particular species may be expected in any given locality.

In the last chapter, topics such as the extirpation of species, recent or proposed reintroduction efforts, and possible occurrence of heretofore unknown species in the state are included.

A current checklist of all Montana mammals is provided at the back of the text so that readers may keep track of the species they have seen. Hopefully this will also serve as encouragement to the reader to work toward observing all 108 species, a noble goal and surely a notable achievement if attained (the author even admits to being several species short of this goal at the time of this publication). Finally the detailed glossary should answer any questions on terminology used throughout this text.

Mammalian Characteristics

Mammals are classified based on the presence of mammary glands (hence the name) for the production of milk to nourish the newborn and the presence of hair. No other taxonomic class of animals possesses these characteristics, so they define the group and are worth considering in detail.

Mammary Glands

Mammary glands are actually modified sebaceous (sweat) glands. The number of mammary glands that form is species-specific. Primates, for example, typically produce 2, while some marsupials may have as many as 24 (and hence have the ability to accommodate larger numbers of offspring). Because most mammals develop in utero and are born in a relatively immature state, they require an immediate source of nourishment before they develop the physical ability and the behavioral skills to search for food on their own. Mammary glands provide this nourishment.

Composition of the secretions produced by the mammary tissue, "milk," is complex and species-specific. Water content can vary from as little as 47% to as much as 87% in species. Remaining components consist of a mixture of lipids, carbohydrates, and proteins.

Hair

The other strictly mammalian characteristic is development of hair. Hair, in its varied modifications, functions in a multitude of ways among which are: 1) as a primary source of insulation, 2) to provide physical protection from abrasion, 3) in tactile sensations such as the vibrissae in felids (cat family), 4) as a means of protective coloration, 5) to provide buoyancy in aquatic species, 6) for protection from predation as with quills and "bony" plates, 7) for locomotion, and 8) in a variety of behavioral activities.

Cardiovascular and Respiratory Systems

The cardiovascular and respiratory systems of mammals also have become highly specialized and variable throughout the course of evolution. Mammals possess a 4-chambered heart, with complete separation of oxygenated and unoxygenated blood, providing an efficient delivery system for required nutrients and gases. The respiratory system is highly partitioned into blind-ending sacs, or alveoli, giving the lungs a tremendous surface area for gaseous exchange. Many mammals maintain a constant body temperature and are thus referred to as homeothermic. However, these metabolic parameters can be adjusted by many species to offset energetic demands created by colder temperatures. Many Montana mammals can, and do, exhibit either torpor or true hibernation when winter sets in. The ability to alter body temperature is referred to as heterothermy. Here, heart and respiratory rates are allowed to drop, placing the animal in a reduced metabolic state. In true hibernation, the animal's body temperature may actually drop to near ambient temperatures (1°C within a nest). Hibernation has become most highly developed in rodents, among which marmots, ground squirrels, and chipmunks demonstrate the greatest ability. Some bats also demonstrate this physiological modification.

Torpor, a condition in which the temperature of the body falls to a lesser extent than in hibernation (generally a few degrees to nearly 20°C), still provides a significant reduction in metabolic costs to the animal.

This metabolic adjustment occurs in many Montana species, particularly many rodents and bats, and both bear species, and at least 1 mustelid, the pine marten.

Digestive System

Mammals can be grouped readily into 3 categories based upon their feeding habits and anatomy of their digestive system. In Montana we have representatives of all 3: herbivores, carnivores, and omnivores. Herbivores are vegetarians. Their dentition and digestive capabilities are highly specialized to process plant materials. Ungulates (hoofed mammals) fall into this category as do most rodents, and all lagomorphs (rabbits and hares). Species which eat meat almost exclusively are termed carnivores. Again many anatomical modifications, such as carnassial teeth (explained below) have evolved for this feeding strategy. Canids (dog family), felids (cat family), and mustelids (weasel family) fall into this category as do the soricids (shrew family), and vespertilionids (bat family). That leaves omnivorous species which are more generalists than specialists, capable of, and preferring, a mixture of both vegetation and meat. The black and grizzly bears have adopted this strategy, as has the raccoon.

Reproductive Biology

All mammals in Montana are placentals, or eutherians, exhibiting internal fertilization and development in utero. The reproductive biology and strategy of Montana's mammals is characterized by the timing of mating activity, length of gestation, number of young born, and number of litters/year. These parameters vary greatly among the state's 108 species.

Most species of mammal in Montana mate during a particular time of the year defined as the mating season and are thus referred to as seasonal breeders. Mating during this time takes place when the female is behaviorally and physiologically receptive to the male. A few species do not display seasonal mating, and are reproductively active year-round.

Skeletal and Dental Systems

For the purposes of species identification, skeletal and dental characteristics are probably of most importance. These tissues, particularly teeth, are the hardest of body structures and are capable of fossilizing. For this reason, they are more commonly found and available for identification. Over the course of evolution in some species, the mammalian skeleton has become stronger through the reduction in number of bones and the fusion of many that have remained.

The most significant diagnostic characteristics used for taxonomic purposes are the structure of the skull and its associated teeth. A typical adult mammalian skull contains 22 bones. Size and conformation of these bones and the nature of the dentition are used extensively in taxonomic keys for species identification. A great deal can be learned about an animal and its feeding habits from a study of these structures.

Teeth

Mammalian teeth are characteristically described based upon the function they perform. In the broadest of categories they can be used to either cut food or to grind and crush it. All mammals in Montana have heterodont dentition, that is not all of the teeth are of a similar size and shape. These differences in tooth structure provide for differences in function. The front teeth, called incisors, are for nipping; deer use these to cleanly cut vegetation; coyotes use them to strip muscle from bone. Immediately behind the incisors lie the canine teeth, numbering a total of 4 (1 on each side above and below). This form of tooth can be greatly enlarged, as in the Family Canidae (the dog family, hence the name),

and can be specialized for grasping, puncturing, and tearing meat. They serve not only for feeding but for protection. All carnivores possess enlarged canines; reduced forms may be present and less functional in some artiodactyls, notably elk. The remaining teeth in the skull may or may not be easily distinguished in the adult, although they are developmentally different. These teeth are referred to as the molariform teeth and can be divided into premolars and molars.

Premolars lie between the canines and the true molar teeth within the cheek. They are generally smaller, with a less complex root system and cusp pattern. They also are deciduous, which means that they are replaced during the animal's life; often they are described as milk teeth because they are replaced after the newborn is weaned. True molar teeth are characterized by being larger, possessing a more substantial root system, often more complex and numerous cusps, and by being nondeciduous. Occlusal surfaces of these teeth also are important for identification purposes. These teeth primarily serve the function of grinding and crushing food, although in some species, notably members of the families Felidae and Canidae, they can be highly specialized for cutting and shearing food.

Understanding the dental formula.— Mammals are bilaterally symmetrical which means that when divided along the midline from head to toe they have right and left sides which are mirror images of one another, left and right hands for example. This symmetry is evident in the development of the tooth rows; the jaw or cranium contains equally paired teeth, half of which appear on the right side and half on the left. Rather than write a formula which denotes every tooth present in a particular species, mammalogists developed a short-hand method which identifies the type of tooth present (incisor, abbreviated i; canine, c; premolar, p; molar, m) and the number of each type, on 1 side of the head. As an example, the dental formula for the mountain lion (*Puma concolor*) would be written: incisors 3/3, canines 1/1, premolars 3/2, molars 1/1 (or i 3/3, c 1/1, p 3/2, m 1/1, total 30). This indicates that on each side of the head are 3 incisors in the skull (denoted left of the backslash) and 3 in the jaw (denoted right of the backslash). Similarly 1 canine occurs in the upper jaw and 1 in the lower jaw, and so forth [a 0 above or below the backslash would indicate that particular type of tooth was not present in the species as an adult]. The total number of teeth for the mountain lion would thus be 30, 2 times the sum of the dental formula to reflect both sides of the head. Often, as is the case of marmots (*Marmota* sp.) or shrews, it is quite difficult to distinguish between types of teeth, premolars and molars in the former groups, incisors, canines, and anterior premolars in the latter. In this situation the dental formula may reflect this fact either by simply combining both types of teeth or by designating a more generalized type. In the case of marmots premolars and molars may be combined and the formula written as i 1/1, c 0/0, P+M 5/4, total 22. In shrews it is not even entirely clear what the developmental history of the single-cusped teeth are; here the choice has been to designate such teeth as unicuspids and group them together. For the pygmy shrew the formula would be written i 3/1, u 5/0, p 1/2, m 3/3, total 36. Many additional pattern variations exist which are beyond the scope of this book. For a more detailed discussion refer to the companion text: *Key to the Mammals of Montana* (Foresman 2001).

Common External Measurements

When specimens are captured or collected, 5 body measurements are commonly taken: total length, tail length, length of the

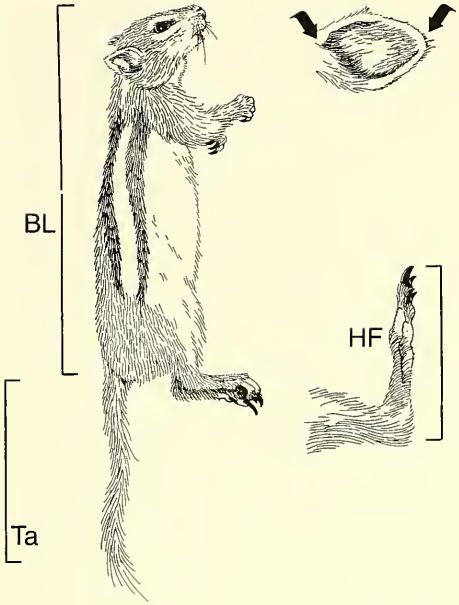


Fig. 1. Common body measurements taken on fresh specimens. Golden-mantled ground squirrel (*Spermophilus lateralis*) pictured. (ear measurement between arrows; HF = hind foot; TL = total length, BL + Ta; Ta = tail length; BL = body length; Head should be extended forward to a flat position).

hind foot, ear length, and body mass (Fig. 1).

Total length (TL): Distance from tip of nose to end of vertebral column in the tail (excluding the extended hairs).

Tail length (Ta): Distance from base of tail to end of vertebral column (excluding the extended hairs).

Length of hind foot (HF): Distance from heal to end of longest claw.

Ear length (E): Distance from base of notch in ear to tip (excluding any hairs).

Mass (M): Presented in either grams (g) or kilograms (kg).

Such standard field measurements, obtained from museum records and field studies, are provided for each species. Where possible, values from a representative sample of 10 adults were averaged for each sex. The actual number of specimens examined is indicated in parentheses following each measurement. All measurements were collected from Montana specimens unless otherwise indicated.

Physiography of Montana

Montana is a land of contrasts. It is the 4th largest state in the union, relinquishing honors only to Alaska, Texas, and California, with a land mass of 380,848 km^2, slightly over 38 million hectares (ha). It lies between 45° and 49° north latitude, placing it squarely within the montane coniferous forest biome. Of this acreage, one-fourth, over 9.3 million ha, is forested (Fig. 2). The remaining three-fourths of the land is dispersed among 4 climatic zones: alpine, subalpine, grasslands, and semidesert (Arno 1979; Craighead et al. 1982; Green and Setzer 1974; Mueggler and Stewart 1974). An elevational gradient within the state runs from 554 m in the northwest corner, where the Kootenai River enters Idaho, to the 3,938 m summit of Granite Peak in the Beartooth Mountains of southcentral Montana.

The state is characterized by mountainous terrain a majority of which lies in the western one-third of the state and serves as the backbone to the Continental Divide (Fig. 2). The Rocky Mountain chain that runs through Montana formed toward the end of the Cretaceous Period of the Mesozoic Era 70–90 $\times$ 10^6 years ago. Several mountain ranges, such as the Bearpaw, Big Snowy, and Crazy mountains, however, are isolated in the central part of the state. These latter mountain ranges were formed more recently, about 50 $\times$ 10^6 years ago, during the Eocene Period of the Tertiary Era (Alt and Hyndman 1986).

As these central mountains were forming, Montana was experiencing 1 of several major dry spells. The combination of uplifting of the continental crust, and sedimentation brought on by soil erosion and the inability of weakly flowing streams to carry suspended materials away, led to filling of the valley floors (Pielou 1991). As we will see later, this, in part, is responsible for the fact that many mammalian species lie isolated on these mountain ranges, unable to disperse across wide-open, lower grasslands.

During the more recent geologic history of the state a series of glacial events greatly influenced distribution of plant and animal communities. Within the past 130,000 years of the Pleistocene Era, 2 major ice ages occurred in Montana (Alt and Hyndman 1986). The 1st, termed the Bull Lake Glacial Period, occurred between 130,000 and 70,000 years ago. The Lauentide and Cordilleran ice sheets extended across Canada just north of Montana and moved southward to cover the valley floors of the northern part of the state (Fig. 3). Higher mountain glaciers also formed on elevated regions of the Beartooth Plateau and what is now Yellowstone National Park. These ice sheets receded only to be followed by a 2nd, more recent ice age, about 15,000 years ago, termed the Pinedale Glaciation, which lasted nearly 5,000 years. These glacial events not only shaped the mountains of western Montana, as is clearly evident in the Mission Mountains just north of Missoula, but they greatly influenced distribution of mammalian populations. Larger species, such as caribou and bighorn sheep, could readily travel at the front of the forming ice sheet, only to move northward again as the interglacial warming periods occurred. Smaller species may have survived in this manner as well, although they also may have chosen to retreat to the mountain peaks which remained free of ice (the term "nunatak" is used to refer to these exposed peaks). In many instances, as conditions warmed and the ice sheets receded, plants and smaller animal species unable to migrate over long distances were left as isolated populations. Species adapted to colder conditions may have been unable to migrate down from their mountain refugia and cross now inhospitable valley floors. Pockets of habitat reminiscent of these colder peri-

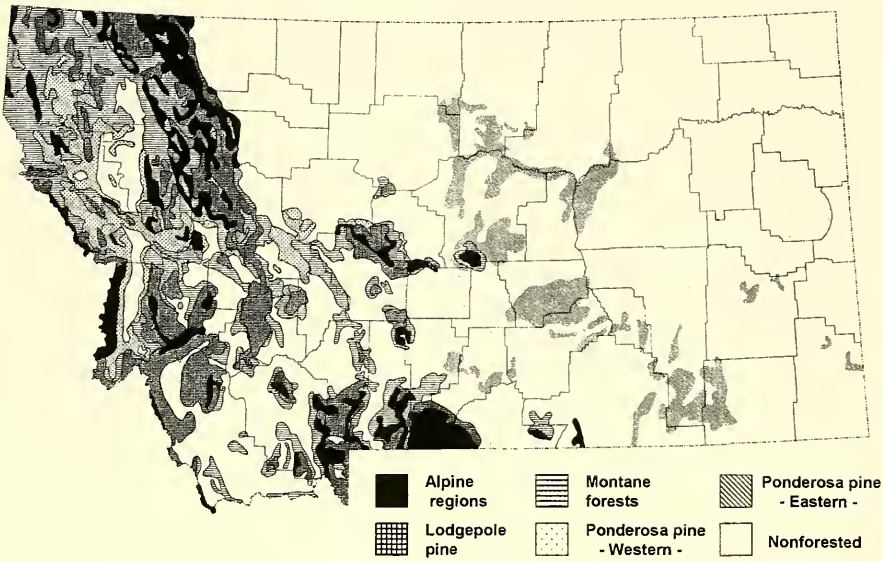


Fig. 2. Forested regions in Montana (after Helburn et al. 1962).

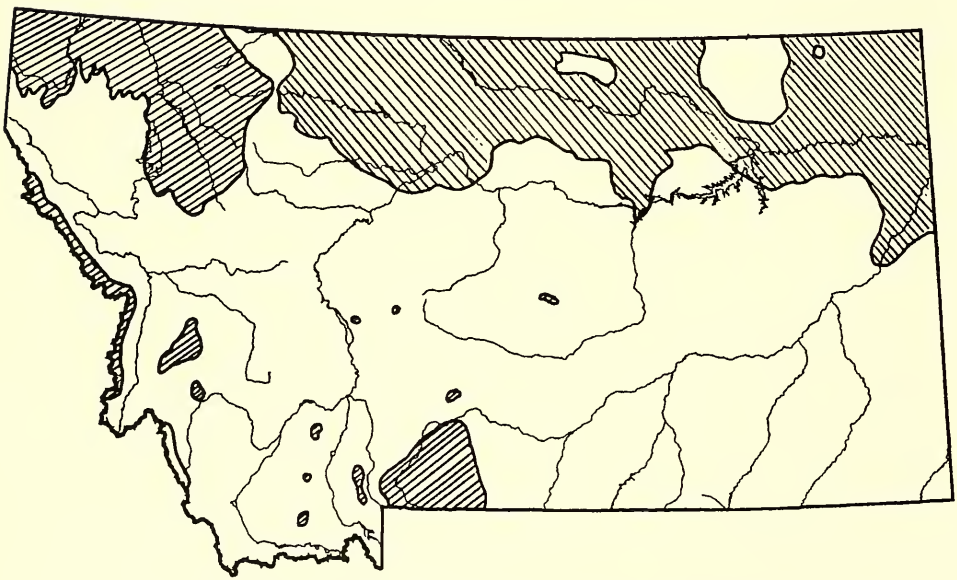


Fig. 3. Major glacial events in Montana over the past 130,000 years.

ods also may have been left as glaciers retreated northward, forcing species adapted to these conditions to remain. These events often explain the present day distributions of mammals that we see, such as the glacial remnant, the northern bog lemming (*Synaptomys borealis*).

More than 80 mountain peaks in Montana exceed 3,385 m, all but 13 of which lie in the Beartooth Mountains in the south-

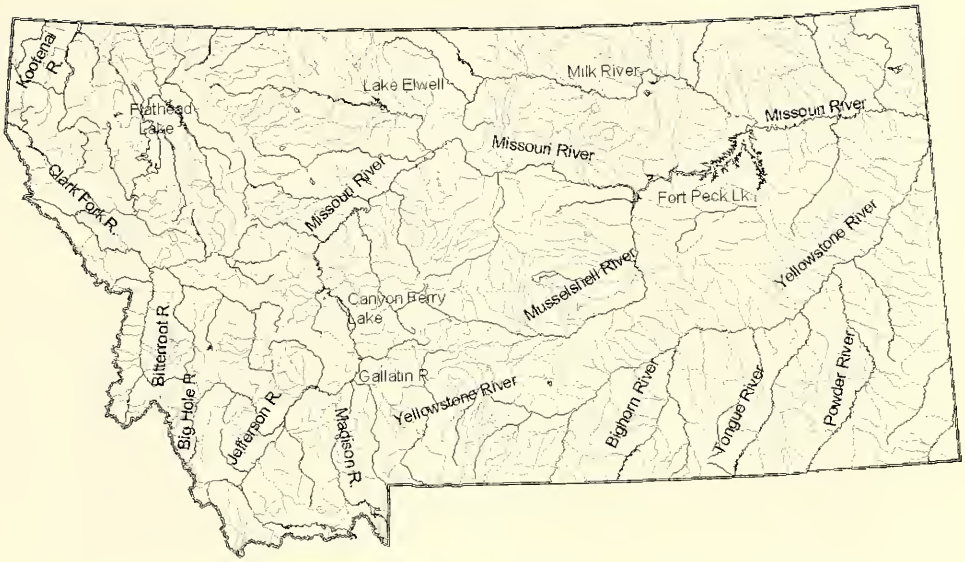


Fig. 4. Major rivers and lakes in Montana.

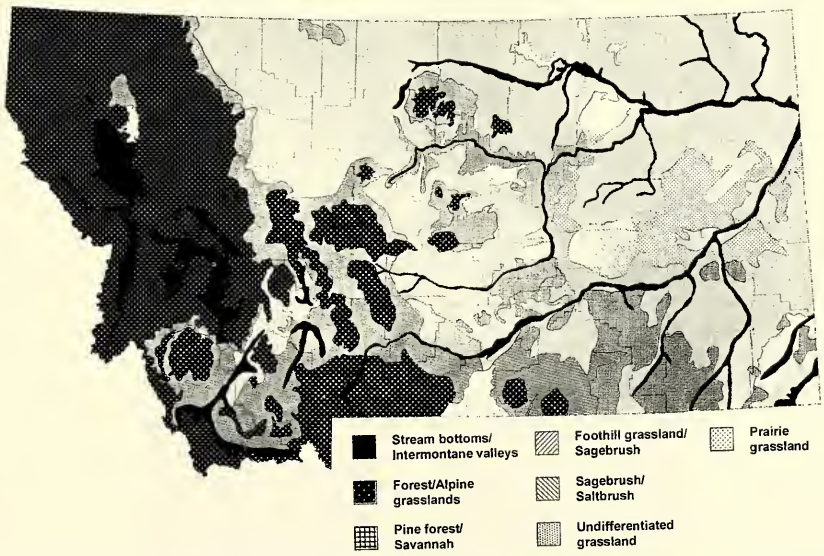


Fig. 5. Vegetation map of Montana illustrating forest and grassland regions (after Helburn et al. 1962).

central part of the state. An additional 498+ peaks exceed 3,077 m, over one-fourth of which are found in the Absaroka Range, directly east of the Beartooth Range and north of Yellowstone National Park (Reese 1985). Interspersed between these mountain ranges lie broad, high-elevation valley systems most of which, particularly in the central and southwestern regions, range between 1,231 and 2,000 m. Native plant communities in these areas are technically classified as steppe grasslands due to the

minimal annual rainfall that they receive. Indeed many of the plant species are similar, if not identical to, those found throughout the steppe highlands of the Tibetan Plateau of Northwestern China, a region lying at a similar latitude.

From the peaks of these mountains, through high elevation plateaus, several major river systems form that dramatically dissect the state (Fig. 4). The most famous of these are the Jefferson, Madison, and Gallatin that converge at Three Forks to form the Missouri, and the Yellowstone, which drains Yellowstone Lake in the National Park flowing northward to merge with the Missouri just across the Montana–North Dakota border. This system ultimately flows into the Gulf of Mexico. In the westcentral part of the state, the Bitterroot and Blackfoot rivers converge with the Clark Fork in Missoula, ultimately draining into the Columbia and the Pacific Ocean. Another smaller system forms in Glacier National Park and drains northeastward into Waterton Lake, then to the Saskatchewan River, finally flowing into Hudson Bay. Because water coming off of Triple Divide Peak here can find its way into any of these 3 systems, it is termed the Triple Divide, and the entire region termed the "Crown of the Continent."

The state is characterized by extremely hot temperatures in summer, particularly in the arid southeast where temperatures in excess of 38°C (100.4°F) are common. Bone-chilling temperatures in the winter are not uncommon (a record temperature of −21°C, −69.8°F, was recorded on Rodgers Pass in 1954). The northwestern region is influenced by coastal air masses from the Pacific and is thus milder and more moist. The northcentral region, which lies on the opposite side of the Continental Divide, routinely suffers under arctic air blasts which sweep down across the mountains of British Columbia and the plains of Alberta. These airflow patterns, and the annual amount and regional distribution of rainfall received, have greatly influenced the vegetative characteristics of the state (Fig. 5). Climatological and physical features, coupled with 1 of the lowest population densities in the country (2.6 persons/km^2; National Geographic Atlas of the World 1990), have shaped the faunal community that we see today.

Montana can be divided into 5 broad, habitat zones (A–E) primarily based upon vegetative characteristics. A closer look at each will provide the background necessary for an understanding of mammal distributions within the state.

Alpine Tundra [Habitat Zone A]

A classification scheme for this category was developed by Craighead et al. (1982) and will be used here. Most easily, this category is recognized as that area which exists above timberline. Within the state, this can be found at varying elevations; it may arise as low as 2,215 m in the northwestern portion of the state although, in general, it occurs at least at, or above, 2,462 m. About 50,000 ha of Montana falls into this category, with a majority of this habitat in the northwestern mountain ranges of the Rocky Mountain chain and the Beartooth Plateau of southcentral Montana. Although a general picture of a landscape devoid of trees comes to mind, quite often this region is defined by clumps of stunted species ("krummholz") such as subalpine fir, white bark pine, and Engelmann spruce. The meadow system that extends up to the rocky talus slopes, and the Mountain Massif itself (bare bedrock), is characterized by a variety of sedges and forbs, with other species appearing depending upon moisture conditions (Fig. 6).

This is a severe, inhospitable region for a large part of the year, a fact that does not go unnoticed by the animal species that attempt to live here. Several species of rodent, notably the hoary marmot and golden-mantled ground squirrel, and 1 lagomorph, the pika or "rock rabbit," have evolved life strategies conducive to this environment.

Fig. 6. Alpine vegetative zone; Habitat Zone A.

Fig. 7. Subalpine vegetative zone; Habitat Zone B.

Fig. 8. Forest Habitat Zone C: Forest Type (a): northwestern Montana; western red cedar, western hemlock, grand fir, and white pine predominate.

Fig. 9. Forest Habitat Zone C: Forest Type (b): westcentral Montana; alpine larch, western larch, and ponderosa pine predominate.

Subalpine Zone [Habitat Zone B]

Lying just below the alpine zone and extending down to timberline, the subalpine zone is characterized by white bark pine, subalpine fir, and subalpine larch, with lesser amounts of Engelmann spruce, western white pine, and Douglas fir, depending upon moisture conditions. Grouse whortleberry, mountain gooseberry, wood rush, arnica, and elk sedge serve as undergrowth dominants. The lower extent of this zone may appear as low as 1,231 m in the northwestern corner of the state, with the upper subalpine zone and timberline zone appearing between 2,000 and 2,215 m, respectively (Pfister et al. 1977). The severity of winter weather conditions in this zone precludes the existence of most mammals, although it often serves as highly productive summer range for species such as mule deer, elk, and bear (Fig. 7).

Forested Regions [Habitat Zone C, Types a, b, c, d, e, f, g]

In terms of defining a general forest habitat classification scheme with which mammal associations might most readily be understood, the "forest regions" concept of Arno (1979) seems most useful. This approach most closely correlates tree species with geographic and climatic characteristics in Montana (Pfister et al. 1977). Given this approach, 7 forest regions have been characterized in this state, although 2 of these, the northeastern and southeastern zones, more specifically reflect grassland biomes (Fig. 2).

In the northwestern part of the state, forests are dominated by western red cedar, western hemlock, grand fir, and western white pine, indicative of the moist maritime influence of the Pacific Coast (Forest type a; Fig. 8). Here, precipitation averages 18–24 cm/year, and temperatures are relatively mild compared with the rest of the state.

North- and westcentral areas reflect the drier conditions of the intermountain region. Alpine and western larches, and ponderosa pine predominate in the westcentral zone, with non-forested areas lying in a mixture of bluebunch wheatgrass and Idaho Fescue grasslands (Forest types b and c; Figs. 9 and 10). Annual precipitation in this region ranges from 12–22 cm, with the higher amounts accumulating in the Bitterroot Mountains south of Missoula.

The northcentral region of the state routinely receives some of the most severe winter weather recorded in the continental United States due to the path of arctic air flow. Near here, the world-record temperature drop over a 24 hour period occurred with a change of 38°C (McWhirter and McWhirter 1972). These conditions preclude the appearance of ponderosa pine but are supportive of extensive quaking aspen and forests of limber pine. To a lesser degree subalpine fir, whitebark pine, lodgepole pine, and Douglas fir occur, all at higher elevations (Forest type d; Fig. 11).

The central region of the state exemplifies forest characteristics consistent with the greater Rocky Mountains. Here Douglas fir, lodgepole pine, and subalpine fir predominate at higher elevations, while ponderosa pine, limber pine, and creeping juniper cover the lower elevations (Forest type e; Fig. 12).

In the southwestern zone Douglas fir and lodgepole pine also characterize the higher elevations. However, nearly three-fourths of this region lies in semiarid steppe sagebrush and bluebunch wheatgrass–fescue grasslands due to the dryness and high elevation characterizing this area (Forest type f; Fig. 13).

The southcentral zone receives much more moisture (14–18 cm annual average) and thus supports a more diverse flora with Douglas fir, lodgepole pine, spruce, and subalpine fir running the elevational gradient. As in zones described above, the lower elevation valleys support a mixture of bluebunch wheatgrass, fescue, and needlegrass grasslands (Forest type g; Fig. 14).

Semidesert [Habitat Zone D]

Parts of 1 region, the Pryor Mountains, due south of Billings along the Wyoming

Fig. 10. Forest Habitat Zone C: Forest Type (c): westcentral Montana grasslands; a combination of bluebunch wheatgrass and Idaho fescue.

Fig. 11. Forest Habitat Zone C: Forest Type (d): northcentral Montana; quaking aspen and limber pine at lower elevations with subalpine fir, whitebark pine, lodgepole pine, and Douglas fir at higher elevations.

Fig. 12. Forest Habitat Zone C: Forest Type (e): central Montana; Douglas fir, lodgepole pine, subalpine fir at higher elevations with ponderosa pine, limber pine, and creeping juniper at lower elevations.

Fig. 13. Forest Habitat Zone C: Forest Type (f): southwestern Montana; Douglas fir and lodgepole pine with steppe grasslands of sagebrush, bluebunch wheatgrass, and needlegrass predominating.

Fig. 14. Forest Habitat Zone C: Forest Type (g): southcentral Montana; Douglas fir, lodgepole pine, spruce, and subalpine fir at the higher elevations with bluebunch wheatgrass–needlegrass grasslands at the lower elevations.

Fig. 15. Forest Habitat Zone D: Semidesert—southeastern Montana—Pryor Mountains; pure stands of ponderosa pine predominated by grasslands of gramas, bluebunch wheatgrass, and needlegrass.

Fig. 16. Grasslands—Habitat Zone E: Yellow willow–beaked sedge–blue joint reedgrass riparian community in eastern Montana.

Fig. 17. Grasslands—Habitat Zone E: Green ash–common chokecherry community in eastern Montana.

Fig. 18. Grasslands—Habitat Zone E: Black cottonwood–red-osier dogwood community along streams in eastern Montana.

Fig. 19. Cultivated land in eastern Montana.

border, are 1 of the most arid areas in the state, receiving only 18 cm of moisture annually. Here, big sagebrush predominates and the grasslands are of a mixed prairie type (Patterson 1985; Fig. 15). Several unique mammals have been recorded here including the pallid and spotted bats (Worthington 1981).

Grasslands [Habitat Zone E]

Northeastern Montana was dominated originally by shortgrass prairie intermixed with cottonwood stands along the Missouri bottomlands and a riparian flora consisting of yellow willow, beaked sedge, and blue joint reedgrass (Hansen et al. 1990). This riparian community (Fig. 16) still exists and also can be found in the central part of the state. Since the late 1800s, most of the native grasslands have been converted into cultivated crops such as wheat and sugar beets.

About 80% of the southeastern part of the state lies unforested as an extension of the Great Plains grassland, with a mixture of gramas, bluebunch wheatgrass, and needlegrass (Fig. 17). Broad river valleys dissect this grassland supporting riparian communities of black cottonwood, red-osier dogwood, green ash, and common chokecherry (Hansen et al. 1990; Fig. 18). Pure stands of ponderosa pine are the rule. Annual precipitation in this region tapers off to a low of 7 cm, and temperatures can range from −1°C in December to 39°C in July. As with the rest of eastern Montana the most fertile grasslands in the valleys are now maintained in corn, sugar beets, and hay (Fig. 19), while the drier sagebrush and cactus badlands, formerly the environs of the buffalo, accommodate cattle, sheep, and coal strip mining. With such a diversity in habitat types, and weather conditions that run the extremes of moisture and temperature, it is not hard to understand why Montana also has such a diverse mammalian fauna.

ORDER INSECTIVORA

The order Insectivora consists of a variety of diverse mammals, from hedgehogs and tenrecs of Africa, Europe, and Asia, and solenodons of Cuba, to the more familiar moles and shrews. Worldwide this order comprises 7 families within which 65 genera and 390 species are recognized. The 3 groups above (solenodons, moles, and shrews) are the only members of this order occurring in North America; in Montana, this order is represented solely by the shrews (family Soricidae). Although moles (family Talpidae) are common in westcentral Idaho, in the extreme southeastern region of Wyoming, and in eastern North Dakota, they have not yet been recorded in Montana.

In general, species within this order are small and have retained many morphologic characteristics representative of the Cretaceous therians from which they evolved (Fig. 20). The ordinal name, derived from a combination of the Latin terms insectum, referring to insect, and voro, which means "to devour," identifies the predominantly insectivorous nature of their feeding habits. Animals other than insects and some plants, however, also may be eaten.

The shrews of Montana (genus *Sorex*, family Sorcidae) are very small, with pointed snouts, small eyes, and thinly furred ears hidden, for the most part, within the fur. The pelage is short, almost velvet-like; all feet have 5 digits, and the tail is long and hairy.

Shrews (collectively known as the soricids) are voracious eaters, requiring 1–2 times their own body weight in food per day. This incredible energetic requirement is a response to the surface-to-volume ratio which such a small size imparts. Because of their extremely small size, they continually radiate a large amount of body heat into the environment. To compensate for this heat loss, and still retain their homeothermic nature, they evolved a high rate of metabolism. This in turn has necessitated the evolution of extremely efficient cardiovascular and respiratory systems. The common shrews of Montana exhibit heart rates approaching 1,000 beats/minute, at rest, and breathe an incredible 800 times/minute. Because of these physiological constraints, they are unable to reduce their body temperature during winter by entering torpor or hibernation (they are unable to store enough body fat to live upon) and thus must forage continuously (the water shrew may be an exception). During winter, heat loss is offset to some degree by their subnivean (under snow) existence. This notwithstanding, their heightened metabolic activity leads to a shortened lifespan, which averages 16–18 months.

Of the 34 species of shrews in North America, north of Mexico, 10 are found in Montana. This large number of species, more than commonly found in most other states, results from the diversity of habitats available within the state.

Family Soricidae—Shrews*

Arctic Shrew
Sorex arcticus

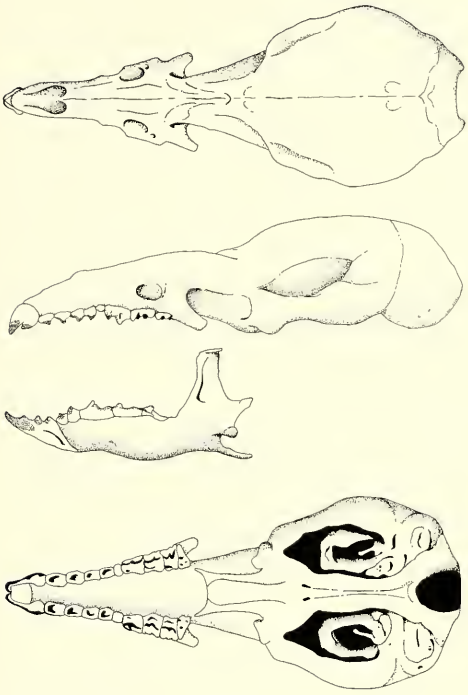
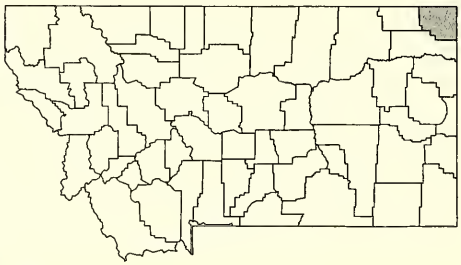


Fig. 20. Skull of a shrew (*Sorex*).



Map 1. Distribution of the Arctic shrew, Sorex *arcticus*.

Scientific Name: This species was first described by Kerr in 1792 from a specimen collected at the mouth of the Severn River, Hudson Bay, Ontario, Canada. The original epithet, *Sorex arcticus,* is still applied today. The generic distinction, *Sorex,* is derived from the Latin, sorex, which means "shrew mouse"; the specific epithet, *arcticus,* is from the Greek arktikos, meaning north or "land of the bear."

Description: This shrew is of medium size for the genus *Sorex,* although 1 of the larger species found in the state, and is distinctly tricolored. The dorsum is dark brown to black set off by lighter brown sides and a grayish-brown venter. Tricoloration may be less distinct in juveniles. The arctic shrew should not be confused with any other soricids in Montana due to its distinctly tricolored appearance, its restricted distribution (see below), and its larger size relative to other sympatric species.

Measurements: [mm(*n*)]: TL = ♂ 70.0(3)/♀ 72(3); Ta = ♂ 45.3(3)/♀ 44.3(3); HF = ♂ 13.5(3)/♀ 13.8(3); E = ♂/♀ no measurements; M [g(*n*)] = ♂ 7.7(3)/♀ 7.87(3). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: The Arctic shrew has a wide distribution that extends across northern North America from the southern Yukon southward through British Columbia and across the Canadian provinces to Nova Scotia. Southern extensions occur from North and South Dakota eastward through Minnesota, Michigan, and Wisconsin. This species was collected for the 1st time in Montana in July 2000, at Medicine Lake National Wildlife Refuge [Sheridan County], in the far northeastern corner of the state (E. Madden and N. Perry, pers. comm.).

* For representative skull characteristics of this taxonomic family refer to Fig. 20.

Ecology and Behavior: Most reports for this species have come from moist sites, predominantly wet meadows, swamps, and marshes. Two localities yielded Arctic shrews, the 1st was the wet meadow zone of a marsh impoundment dominated by quackgrass, sow thistle, baltic rush, and sedges. The 2nd site was located in sandy flats of the flood plain dominated by clustered field sedge, baltic rush, sow thistle, western wheatgrass, and saltgrass. Other species collected at this location included the masked shrew, the meadow vole, the deer mouse, and Richardson's ground squirrel. The sympatry of Arctic shrew with masked shrew has been well documented. These species may have different tolerances for moist conditions with the former preferring a lower water table and the latter a high water table. If this is true, it would partition resources and limit competition.

No information is available on the dietary preference of the Montana population but, as is true of other soricids in the state, it is predominantly insectivorous. A wide variety of aquatic and terrestrial invertebrates are present in such moist sites. The only study to specifically quantify food items consumed by this species found that 60–70% of the stomach contents of individuals sampled (n = 62) in autumn consisted of larch sawfly.

Except for short bouts of rest, the Arctic shrew is active 24 hours a day with greater periods of activity during night. The lifespan of this species may be shorter than other shrews. Juveniles born early in spring reproduce in August and these, as well as adults, appear to disappear by autumn. In this manner 2 generations apparently turn over each year. An 80% mortality may occur by the time sexual maturity is reached. Further study is needed to clarify this unusual pattern.

Reproduction: Although no information is available on the breeding biology of the Arctic shrew in Montana, populations in Minnesota begin reproductive activity in late March to early April. Breeding may continue into August with some individuals producing 3 litters. Gestation length has not been reported but it is most likely 20–21 days as in other soricids. Mean litter size is 6.7 (range = 4–9).

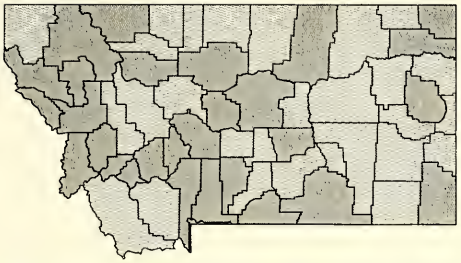
Status: Although this species has just been collected in the state for the 1st time (a total of 6 individuals in July 2000) its status is unknown. Most likely it should be considered uncommon and is thought to be restricted to the far northeastern corner of the state.

Kirkland, G. L., Jr., and D. F. Schmidt. 1996. *Sorex arcticus*. Mammalian Species 524:1–5.

Masked (Common) Shrew
Sorex cinereus

Common shrew (*Sorex cinereus*).

Scientific Name: First collected by J. R. Forster in 1772 at Fort Severn, Ontario, Canada, and later described by Kerr in 1792 as *Sorex arcticus cinereus*. In 1922, Jackson (1922) elevated this subspecies to specific ranking and designated this form as *Sorex cinereus cinereus*. The generic distinction, *Sorex*, is from the Latin, sorex, meaning "shrew mouse"; the specific epithet, *cinereus*, is Latin for "ash-colored," a reference to the color of its pelage.



Map 2. Distribution of the masked shrew, *Sorex cinereus.*

Description: A non-descript species, brownish in color on the dorsal surface and grayish on the ventral side. The vernacular name is not well chosen because no obvious facial mask exists. One of the more distinguishing characteristics is the color of the tuft of hairs at the tip of the tail. When viewed from below, these hairs are black. Until 1980, 2 subspecies of *cinereus, S. c. cinereus* and *S. c. haydeni,* were thought to occur throughout the state. Recent taxonomic studies have elevated *haydeni* to species status (Foresman and Jensen 1992; van Zyll de Jong 1980). The 2 species are very similar and cannot be easily distinguished (refer to above references). Only slight variations in pelage color occurs between the masked shrew and the closely related Hayden's shrew, and its tail is slightly longer. However, the masked shrew can be reliably distinguished from Hayden's shrew only by a detailed analysis of the skull. In Montana it is somewhat larger than Preble's shrew, the other most closely related species with a similar dental pattern.

Measurements: [mm(*n*)]: TL = ♂ 95.1(10)/♀ 93.9(10); Ta = ♂ 39.5(10)/♀ 40.9(10); HF = ♂ 10.3(10)/♀ 11.6(10); E = ♂ 6.0(3)/♀ 5.4(7); M [g(*n*)] = ♂ 3.3(10)/♀ 3.5(10). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: The masked shrew has the largest range of the 34 *Sorex* species in North America and is 1 of the most common species throughout the country and surely in Montana. Its distribution ranges from Alaska to Nova Scotia, across all of the Canadian provinces. Extensions southward into Washington and Idaho continue across the northern one-half of the United States.

Ecology and Behavior: Although this species inhabits a variety of habitats, when it occurs sympatrically with the vagrant shrew it is associated with the drier, coniferous forests, while the latter species is more prevalent in moist regions.

Nests are constructed within decaying logs out of grass and leaves. As with most Montana soricids, preference is given to habitats that have a great deal of ground structural complexity; downed woody material and grass cover. Such an environment provides both secure cover for protection against predation, and a rich source of food.

Masked shrews are primarily insectivorous, feeding on a wide variety of invertebrates from beetles to earthworms. Eggs and pupae of insects are eaten extensively during winter months when other foods are unavailable. Mice, particularly newborns, and salamanders also may be consumed.

Remaining active throughout the year, the masked shrew is constantly on the go, foraging to meet its metabolic requirements. Most activity is confined to nighttime hours (Buckner 1964). A fascinating behavioral pattern, known as "caravanning," exhibited by shrews in the genus *Crocidura,* has been described in this species (Goodwin 1979). When startled, young lit-

Fig. 21. Caravanning behavior in young masked shrews.

termates responded by running in formation, keeping in contact with the individual in front by burying their noses in the rump fur (Fig. 21).

Reproduction: Breeding begins in late March to early April, peaking in May (Foresman and Jensen 1992). Although no breeding has been observed in Montana during the summer or autumn, it probably occurs. Litter size ranges from 2–10. Young are born in an extremely altricial state but are weaned by day 20 and reach maturity rapidly. Sexual maturity is not attained until the animal is 1 year of age. Animals attain an age of 14–16 months in the wild.

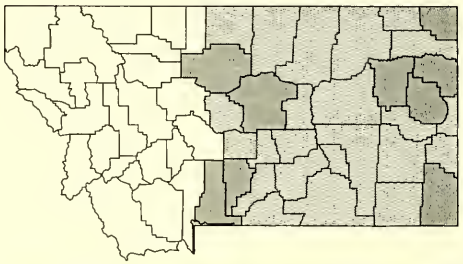
Status: Common in the western half of Montana.

Hayden's Shrew (Prairie Shrew)
Sorex haydeni

Scientific Name: The taxonomic status of this species has come full circle since it was first collected in 1855, in western North Dakota, by F. V. Hayden, and originally described as *Sorex haydeni* by Spencer Fullerton Baird, founder of the United States National Museum, in 1857 (Baird 1857). Taxonomic revisions in 1928 redefined *S. haydeni* as a subspecies of *Sorex cinereus* but recent morphologic and ecological evidence by van Zyll de Jong (1980) in Canada, and Foresman and Jensen (1992) in Montana, has supported its elevation again to specific status. The generic distinction, *Sorex,* is derived from the Latin, sorex, which means "shrew mouse"; the specific epithet, *haydeni,* honors F. V. Hayden.

Description: A small species, with brown dorsal coloration blending into a lighter brown shade on the lateral surfaces, and a more whitish venter giving the slight impression of tricoloration. The tail is shorter than other comparable species, having a tuft of hair on the tip which is brownish when viewed ventrally. This species is difficult to identify in the field, where it is easily confused with the masked shrew. The habitat to which a specimen is associated should be noted carefully, and a detailed analysis of the skull should be made by an expert for positive identification.

Measurements: [mm(*n*); Smith 1993]: TL = ♂/♀ 82.5(17); TA = ♂/♀ 31.9(17); HF = ♂/♀ 11.1(17); E = ♂/♀ 7.7(17); M [g(*n*); Hall 1981] = ♂/♀ = 3.3(17). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.



Map 3. Distribution of Hayden's shrew, *Sorex haydeni.*

Distribution: Hayden's shrew occurs across the southern Canadian provinces of Alberta, Saskatchewan, and Manitoba, southward across eastern Montana to Nebraska and Missouri.

Ecology and Behavior: Along the northernmost range of its extension in the Canadian provinces, Hayden's shrew prefers drier, grassier habitats than those to which the masked shrew is associated (Foresman and Jensen 1992; van Zyll de Jong 1980). Evidence suggests that, where sympatric with this latter species, habitat segregation occurs.

As is true of most soricids, Hayden's shrew consumes a wide variety of insects, earthworms, and small vertebrates. Little

additional information is available for this species, although it may be assumed to have many ecological similarities to *S. cinereus.*

Reproduction: Breeding probably occurs from March through possibly July or August, with litter sizes averaging 3–6 young.

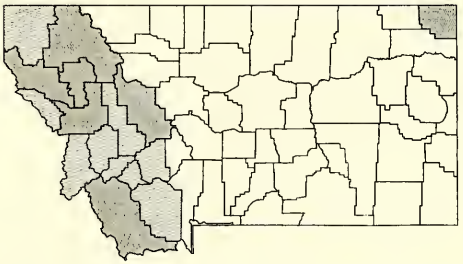
Status: Common.

Pygmy Shrew
Sorex hoyi

Scientific Name: First described in 1858 by Spencer Fullerton Baird from a type specimen collected in Racine, Wisconsin. Initially identified as *Sorex hoyi,* a revision to the distinct generic status of *Microsorex hoyi* was supported by Jackson (1925). Recently a detailed systematic analysis reduced this generic status to the subgeneric level reestablishing the original name. The generic name, *Sorex,* is derived from the Latin, sorex, meaning "shrew mouse"; the specific epithet, *hoyi,* honors an early 19th century naturalist, Dr. Phila Romayne Hoy.

Description: This species vies with the tiny shrew, *Sorex minutissimus,* a Eurasian species most recently found in Alaska, and Kitti's hog-nosed bat (the "bumble bee bat" of Thailand) for honors as the world's smallest mammal, thus the vernacular distinction. In Montana the average weight is 2 g (in comparison a penny weighs 3 g). Pelage is grayish-brown on the dorsal surface, blending into a lighter whitish gray ventral surface. In hand, the pygmy shrew easily could be confused with the other, smallest of Montana soricids (the masked shrew, dwarf shrew, and Preble's shrew). A close look at the unicuspid toothrow is necessary to make this distinction.

Measurements: [mm(*n*)]: TL = ♂ 79.1(10)/♀ 83.4(7); Ta = ♂ 27.9(10)/♀ 21.6(7); HF = ♂ 9.5(10)/♀ 9.6(7); E = ♂ 2.0(2)/♀ 3.0(1); M [g(*n*)] = ♂ 2.6(9)/♀ 2.4(7). Dental formula: i 3/1, u 5/0, p 1/2, m 3/3, total 32.



Map 4. Distribution of the pygmy shrew, *Sorex hoyi.*

Distribution: Pygmy shrews are widely distributed from Alaska, across the Canadian provinces southward, extending across eastern Washington, northern Idaho, and western Montana. Its distribution dips across the Dakotas eastward, extending across the northern United States to the East Coast. Populations, likely isolated by early glacial events, are found in the southern Appalachians. This species was not captured frequently in Montana until 1988 (Foresman 1999).

Ecology and Behavior: Although dry, open coniferous forests (ponderosa pine, western larch) appear to be the preferred habitat, individuals have been collected from dense mesic Douglas-fir forests in the Bitterroot Mountains of Idaho bordering Montana and the sagebrush shrub steppe plateau of the Big Hole National Battlefield. To date, only 61 individuals have been captured in Montana.

This species is strictly insectivorous, preferring a diet of insect larvae, beetles,

moths, spiders, and flies. As with other shrews, it needs to eat 1–2 times its own body weight in food each day to offset its extremely high metabolic rate. Although little life-history information is available for the pygmy shrew, it can be assumed that its general ecological needs are similar to those of other soricid species.

Reproduction: In Montana, the pygmy shrew is known to produce litters in the spring and early summer and is capable of breeding more than once during this period (Foresman 1986). Litter size varies from 3–6, with young attaining adult size by winter. Typically, this species would live 16–17 months.

Status: The pygmy shrew should be considered a species of special concern. Although it is common throughout its northern and eastern extensions, it is clearly not abundant in Montana.

Long, C. A. 1974. *Microsorex hoyi* and *Microsorex thompsoni*. Mammalian Species 33:1–4.

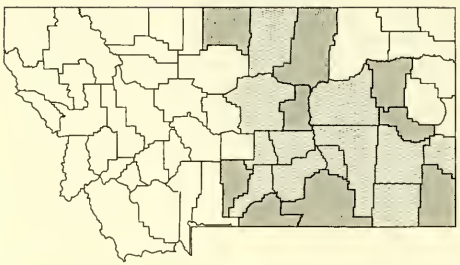
Merriam's Shrew
Sorex merriami

Scientific Name: The type specimen of Merriam's shrew was collected by C. E. Bendire, in 1884, on the Little Bighorn River, near Fort Custer, Montana (Bighorn County). The generic distinction, *Sorex*, is from the Latin, sorex, which means "shrew mouse"; the specific epithet, *merriami*, is in honor of C. Hart Merriam, the 1st Chief of the United States Biological Survey.

Description: Merriam's shrew is markedly lighter in color than any other shrew in the state and is thus easily identified by its light gray dorsal surface, which is sharply demarcated from white medial and ventral surfaces. It also possesses distinctive incisors, which lack a medial tine. Because of distinctive pelage and dental characteristics, and a preference for sagebrush-grass habitats, this species should not be confused easily with other Montana soricids.

Measurements: [mm(*n*)]: TL = ♂ 88.5(2)/♀ 97.5(4); Ta = ♂ 33.0(2)/♀ 37.0(4); HF = ♂ 11.5(2)/♀ 11.8(4); E = ♂ 4.5(2)/♀ 6.9(4); M [g(*n*)] = ♂ 3.3(2)/♀ 3.9(1). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: Since Merriam's shrew has been collected only rarely throughout the Great Basin, Columbia Plateau, parts of the Great Plains, and southeastern Rocky Mountains (Junge and Hoffmann 1981), its true distribution is not well understood. It has been collected in the state only sporadically since 1894. Only 9 specimens have been collected to date.



Map 5. Distribution of Merriam's shrew, *Sorex merriami*.

Ecology and Behavior: All specimens have come from dry sagebrush or sagebrush-grass habitats from the central, to the southeastern part of the state. It is considered to be 1 of the most xeric-adapted shrews in North America. Caterpillars make up the bulk of the diet in the warmer months, with beetles, crickets, and a variety of other insects being consumed during the rest of the year. This species undergoes both spring (April) and autumn (October) molts.

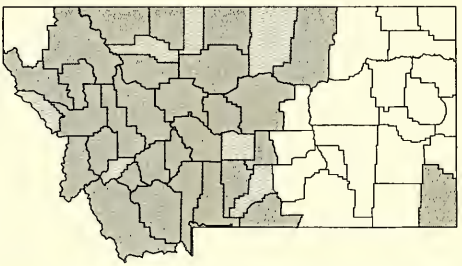
Reproduction: Breeding is thought to occur from mid-March to early July. Litter sizes probably average 5–7.

Status: Uncommon. Primarily in the central and eastern regions. Efforts to capture Merriam's shrew in xeric habitats, however, may demonstrate it is more common than previously thought.

Armstrong, D. M., and J. K. Jones, Jr. 1971. *Sorex merriami.* Mammalian Species 2:1–2.

Montane Shrew (Dusky Shrew)
Sorex monticolus

Scientific Name: The montane shrew was first collected by 2 of the most prominent mammalogists of the late 1800s, C. Hart Merriam and Vernon Bailey, both of whom were instrumental in establishing the field of mammalogy as we know it today. Both individuals were involved in the United States National Museum's Biological Survey, traveling extensively into the western states to enhance the vertebrate collections of this country. The type specimen was collected in 1889, in Coconino County, Arizona, and described as *Sorex monticolus* the following year. Since then, the taxonomic status of this species has been often debated; for much of this time it has been considered either a subspecies of the vagrant shrew, *S. v. monticolus*, or given distinct species ranking as *S. obscurus*. The most recent resolution reestablishes specific status for *monticolus*. The generic designation, *Sorex*, is from the Latin, sorex, meaning "shrew mouse"; the specific epithet, *monticolus*, is from the diminutive form of the Latin mons, monticulus, which means "belonging to (inhabiting) mountains."



Map 6. Distribution of the montane shrew, *Sorex monticolus*.

Description: The color pattern of the montane shrew is similar to that described for many other Montana species; brownish along the back and somewhat more grayish on the belly. The montane shrew is the largest member of the *vagrans* complex, characteristically possessing a larger skull, broader through the interorbital region and longer through the palate. It is easily distinguished from other sympatric species by a combination of unique dental characteristics. A difference in the number of friction pads on the 2nd to 5th digits of the hind feet distinguish this species from the vagrant shrew (Foresman 2001), as does its slightly longer tail.

Measurements: [mm(n)]: TL = ♂ 104.5(10)/♀ 98.6(7); Ta = ♂ 45.8(10)/♀ 44.7(7); HF = ♂ 12.7(10)/♀ 12.0(7); E = ♂ 6.5(10)/♀ 6.0(2); M [g(n)] = ♂ 4.7(10)/♀ 4.7(10). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: The vernacular name of the montane shrew denotes its predominant association with more mountainous regions of North America. Its range extends from Alaska, across the western half of Canada southward, being found in disjunct localities from the Pacific Coast to western Montana, and as far south as northern Mexico.

Ecology and Behavior: The montane shrew is adapted to the montane region

more than is the vagrant shrew, and is able to withstand drier, more acidic soil conditions. Where these 2 species are sympatric, the vagrant shrew is more closely associated with mesic characteristics of the habitat, while the montane shrew is found further from such sources. Although extensive overlap may occur between these 2 species, little evidence suggests that hybridization occurs.

The diet consists primarily of insects and earthworms although, as with other Montana shrews, the montane shrew is quite opportunistic and would be expected to take advantage of other small vertebrates as well.

Home range size has been estimated at slightly over 1,200 m^2 during the nonbreeding period. For both males and females this area increases in size during the breeding season (males = 5,978 m^2; females = 2,226 m^2). Subtle differences in habitat preference appear to segregate the montane shrew from the vagrant shrew. Such preferences may have biological underpinnings, as the more robust skull and teeth of the montane shrew, and the harder nature of its teeth, may allow it to take fuller advantage of chitinous prey.

Two molts occur, 1 each in spring and late summer.

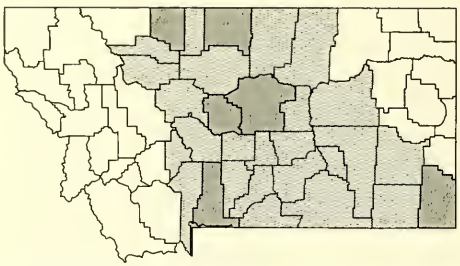
Reproduction: Testicular development probably begins in February; ovarian development is slightly later with mating beginning in March. Up to 3 litters may be expected during spring and summer, with litter sizes averaging 5. Timing of mating is highly influenced by seasonal weather and elevational differences. The montane shrew may attain an age of 18 months in the wild.

Status: Common in the western one-third of Montana.

Smith, M. E., and M. C. Belk. 1996. *Sorex monticolus.* Mammalian Species 528:1–5.

Dwarf Shrew
Sorex nanus

Scientific Name: Originally described as a subspecies of the Inyo shrew, *Sorex tenellus,* by C. Hart Merriam, *nanus* was elevated to species rank, in 1928, by H. H. T. Jackson. The type specimen was collected by E. A. Preble, in 1895, in Estes Park, Colorado, as part of the United States National Museum's Biological Survey of this region. The generic distinction, *Sorex,* is from the Latin, sorex, which means "mouse shrew"; the specific epithet, *nanus,* is from the Latin, nanus, which means "dwarf."



Map 7. Distribution of the dwarf shrew, *Sorex nanus.*

Description: As with most other Montana shrews, dorsal coloration is dark brown, with a sharply demarcated buffy-grayish ventral surface. Winter pelage may be somewhat more gray on the dorsal surface. As the vernacular name implies, the dwarf shrew is extremely small. Superficially, the dwarf shrew could be confused with other, small shrews in Montana. Dental analyses however will readily distinguish it from all but the vagrant shrew and the water shrew; it can be distinguished from these based upon size.

Measurements: [mm(*n*)]: TL = ♂ 91.0(3)/♀ 97.3(3); Ta = ♂ 40.0(3)/♀

42.0(3); HF = ♂ 10.8(3)/♀ 10.5(3); E = ♂ 13.6(2)/♀ 13.5(2); M [g(*n*)] = ♂ 2.5(1)/♀ 2.5(1). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: The dwarf shrew is distributed from northcentral Montana, directly southward through Wyoming, Utah, Colorado, New Mexico, and Arizona, with a slight eastward extension into southwestern South Dakota. Only 20 specimens have been collected in Montana to date. Of these, most have been obtained from higher montane slopes although a few have been collected at lower elevations. Individuals also have been collected more recently in lower elevation riparian and sagebrush-grass vegetation habitats. From these Montana records, and those from neighboring states, the dwarf shrew appears to be adapted to a wide variety of habitat conditions.

Ecology and Behavior: Little information exists on the ecology or behavior of the dwarf shrew. It has been shown to consume spiders and insects in captivity.

Reproduction: No published information exists for reproduction, but limited unpublished data suggests that breeding occurs in late June to early July at higher elevations. First litters have been observed in late July to early August and, with an apparent post-partum estrus, 2nd litters would thus be born in late August to early September (Hoffmann and Owen 1980). Individuals inhabiting lower elevations may breed at an earlier date. Litter size averages 6.5.

Status: Until proven otherwise, this species should be considered rare.

Hoffmann, R. S., and J. G. Owen. 1980. *Sorex tenellus* and *Sorex nanus*. Mammalian Species 131:1–4.

Northern Water Shrew
Sorex palustris

Northern water shrew (*Sorex palustris*). See plate 1.

Scientific Name: The water shrew was first described in 1828, by Richardson (1828), from a type specimen collected in Central Canada. The generic designation, *Sorex*, is from the Latin, sorex, which means "shrew mouse"; the specific epithet is from the Latin, paluster, which means "marshy," a reference to this species' preferred habitat.

Description: The water shrew is the largest insectivore in Montana and the 2nd largest in North America. Individuals may weigh >18 g. It is 1 of the most distinctive soricids, not only for its size, but for its coloration and anatomical adaptations for semiaquatic existence. In Montana, the water shrew is dark black dorsally, with a sharply demarcated silvery-white, to grayish, ventral surface. Hind feet are large and possess stiff hairs between the digits to enhance their paddle-like capabilities (Fig. 22). Because of the size of the water shrew, its distinct coloration pattern and anatomical specializations, and its semiaquatic nature, there should be no confusion with other sympatric species.

Measurements: [mm(*n*)]: TL = ♂ 154.2(10)/♀ 148.4(10); Ta = ♂ 73.8(10)/♀ 74.1(10); HF = ♂ 20.3(10)/♀ 10.1(10); E = no measurements; M [g(*n*)] = ♂ 14.8(10)/♀ 13.5(10). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

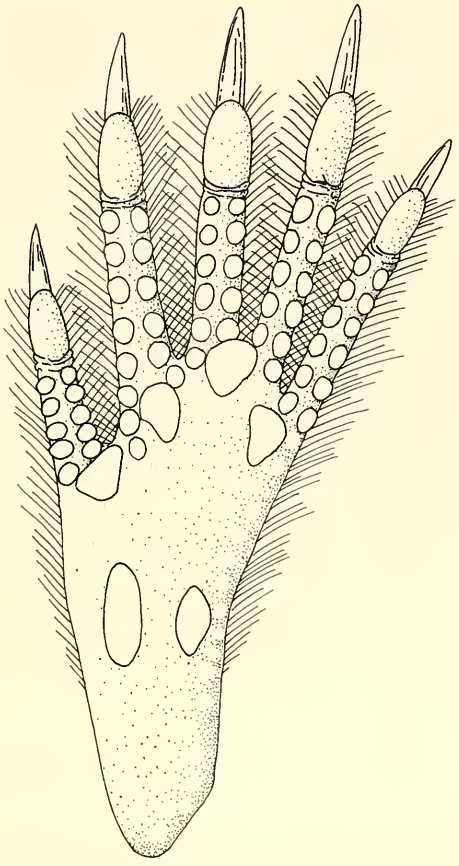
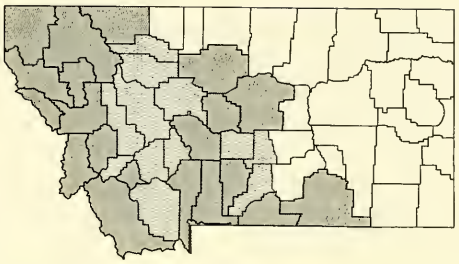


Fig. 22. Anatomical adaptations for a semi-aquatic lifestyle in the northern water shrew.



Map 8. Distribution of the northern water shrew, *Sorex palustris.*

Distribution: The water shrew is widely distributed from southern Alaska, across British Columbia and Alberta, extending over the western one-third of the United States in more mountainous regions. In Montana, it ranges from the valley floor along Rattlesnake Creek near Missoula, to the Beartooth Plateau (Park County) at an elevation of 3,050 meters, and is found in the isolated mountain ranges of central Montana.

Ecology and Behavior: As its name implies, this semiaquatic species prefers stream systems, particularly fast-flowing, cascading, mountain streams. Nests, constructed from leaves and moss often on islands within the stream, are entirely enclosed and are entered by the animal burrowing through the sides (Smith 1993). Water shrews are highly adept swimmers. They have been observed to swim under the ice in winter and are purported to be able to walk on the water surface by trapping air bubbles in the hair of their hind feet (Fig. 22).

The water shrew is an opportunistic feeder, as are most shrews. Although a high percentage of the diet (up to 80%) appears to be aquatic insects, snails, slugs, earthworms, leeches, small fish, larval salamanders, and mice have also been reported as food items. Caching behavior occurs and may be a common phenomenon for most soricid species.

Some evidence suggests that water shrews may lower their body temperature daily and enter a torpid state. Such a physiological capability would be advantageous for a species which feeds continuously in cold mountain streams.

Reproduction: Reproductive maturity is reached in the 1st winter of life, earlier than for other Montana soricids. Testicular enlargement and spermatogenesis begins in late December to early January. Females exhibit ovarian activity beginning in January, with 1st pregnancies in late February. A few individuals can breed their 1st summer, although, more commonly, animals wait until their 2nd spring of life. Gestation is thought to be 20–21 days in length, with up to 3 litters produced in a season. Litter sizes in Montana average 6.

Status: Locally common throughout the mountains.

Beneski, J. T., and D. W. Stinson. 1987. *Sorex palustris.* Mammalian Species 296:1–6.

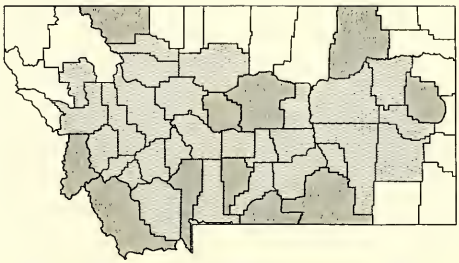
Preble's Shrew
Sorex preblei

Scientific Name: Preble's shrew, named after E. A. Preble who collected the type specimen in Malheur County, Oregon, in 1915, for the United States National Biological Survey, is another extremely small shrew, about the size of the pygmy shrew and the dwarf shrew. The generic designation, *Sorex*, is from the Latin, sorex, which means "shrew mouse"; the specific epithet, *preblei*, honors E. A. Preble.

Description: Preble's shrew has a brownish dorsal surface (more grayish in winter), giving way to a more silvery ventral surface and is distinguished by a bicolored tail. Since Preble's shrew is associated more closely with arid sagebrush and shrub-grass habitats it would rarely, if ever, be found in sympatry with other small species in the state. Great similarities exist between this species and the other members of the *cinereus* complex (*cinereus* and *haydeni*). Where Preble's shrew overlaps with either of these species, it consistently will be the smaller of the 3. Preble's shrew can not be identified reliably without a detailed analysis of skull morphology and comparison with established museum collections.

Measurements: [mm(*n*)]: TL = ♂ 89.0(1)/♀ 92.0(1); Ta = ♂ 36.0(1)/♀ 38.0(1); HF = ♂ 10.5(1)/♀ 11.5(1); E = ♂ 6.0(1)/♀ 5.0(1); M [g(*n*)] = ♂ 2.3(1)/♀ 3.1(1). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: Preble's shrew occurs from eastern Washington to eastern Montana, southward to a band across northeastern California, the northern portion of Nevada, Utah, and southwestern Wyoming. In Montana only 16 individuals have been collected, the largest number (6) from Silver Bow County.



Map 9. Distribution of Preble's shrew, *Sorex preblei*.

Ecology and Behavior: Due to the rarity of Preble's shrew, little published information is available which relates to its ecology. This species prefers arid and semiarid grass and sagebrush habitats across Montana, either in open expanses or in smaller openings within subalpine coniferous forests. However, it has been collected in marsh habitats and stands of lodgepole pine–alpine fir, white fir–spruce, and lodgepole–huckleberry. There is no published information on the feeding ecology of Preble's shrew. Skull and mandibular morphometric studies, however, indicate that the "bite force" that this species can generate is less than other soricid species. This suggests that Preble's shrew may prefer soft-bodied prey.

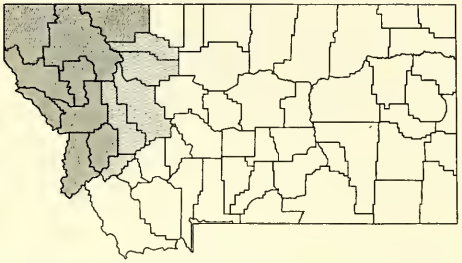
Reproduction: The breeding biology of Preble's shrew is unknown. As with other Montana soricids, however, this species may breed from late spring through mid-summer. At lower elevation, breeding may be extended in more arid localities. Gestation is most likely 20–21 days.

Status: Because only 16 specimens have been collected in Montana, this species must be considered rare until proven otherwise. This "rarity" may be due to the collection efforts and trapping methods employed to date.

Cornely, J. E., L. N. Carraway, and B. J. Verts. 1992. *Sorex preblei*. Mammalian Species 416:1–3.

Vagrant Shrew
Sorex vagrans

Vagrant shrew (*Sorex vagrans*). See plate 1.



Map 10. Distribution of the vagrant shrew, *Sorex vagrans*.

Scientific Name: The vagrant shrew was first described by Spencer Fullerton Baird in the Reports of the Pacific Railroad Survey based upon a type specimen collected by J. G. Cooper, at Willapa Bay (Shoalwater Bay) in Pacific County, Washington. Populations of the vagrant shrew, like those of the masked shrew, recently have been critically studied and, as a result, have subsequently undergone taxonomic revision. Until 1977, 2 subspecies were recognized in Montana, *S. v. vagrans* and *S. v. monticolus*. Following extensive morphometric analyses, *S. v. monticolus* was elevated to specific status (see species description above). The generic designation, *Sorex*, is from the Latin, sorex, which means "shrew mouse"; the specific epithet, *vagrans*, is from the Latin, vago, which means "to wander."

Description: The vagrant shrew is medium-sized, brownish in color along the dorsal surface, blending into a lighter grayish color on the venter. As with most species of shrew, the vagrant shrew is relatively non-descript in hand and thus difficult to distinguish from other sympatric species. It can be distinguished from the montane shrew by counting the number of friction pads on the 2nd to 5th digits on the hind feet (Fig. 22). In general it is slightly smaller in stature than the montane shrew; the greatest distinguishing characteristic between these forms being the degree of pigmentation on the medial tines of the incisors. Considerable sympatry occurs between these 2 species along the western border of Montana and into Idaho and Washington. East of the Continental Divide the montane shrew predominates. The vagrant shrew can be distinguished from the other, most common associate, the masked shrew, by its somewhat larger size, its preference for more mesic habitats, and the nature of its unicuspid toothrow.

Measurements: [mm(n)]: TL = ♂ 107.6(10)/♀ 108.4(10); Ta = ♂ 44.2(10)/♀ 47.0(10); HF = ♂ 12.0(10)/♀ 11.9(10); E = ♂ 6.4(8)/♀ 7.9(7); M [g(n)] = ♂ 5.6(10)/♀ 5.0(10). Dental formula: i 1/1, u 5/0, p 1/2, m 3/3, total 32.

Distribution: The vagrant shrew is found throughout the Columbia Plateau and the Snake River Plains. Its range extends over the northern portion of the Great Basin, eastward to the Continental Divide, and westward to the Pacific Coast.

Ecology and Behavior: Because of the abundance of the vagrant shrew across the northwestern United States, much is known about its ecology. A variety of habitats throughout its range are used, from densely forested sites to more open meadows. A preference appears to be given to mesic sites within the habitat and, where sympatric with other species, particularly

Fig. 23. Feeding behavior of the vagrant shrew where a worm becomes a handful.

the montane and masked shrews, it is suggested to be the stronger competitor for resources.

Non-breeding individuals use a home range of slightly over 1,000 m^2, expanding this to over 3,200 m^2 during the breeding season, with male home ranges exceeding those of females. Territorial behavior develops during the 1st summer, both with other members of the same species (intraspecific competition), as well as between this and other species (interspecific competition). This presumably provides an individual with the food resources required to overwinter. Such behavior ceases through the following spring when breeding commences, however, individuals remain solitary.

The diet consists of a wide variety of insects, particularly adult and larval beetles, and earthworms, spiders, snails, and a lesser amount of plant material (Fig. 23). This species typifies the generalist feeding preference found in most shrews and the opportunistic foraging strategy. Some species, such as the least shrew and the short-tailed shrew are known to cache food for later use, a strategy quite appropriate for a group that must feed nearly continuously.

An interesting capability which the vagrant shrew exhibits is the ability to use echolocation, a phenomenon more closely associated with bats (for a more detailed discussion of echolocation refer to the next section on the order Chiroptera). The vagrant shrew is capable of producing high frequency sounds, in the 18–60 kHz range, whose echoes can then be used to "view" the environment. Under tightly controlled laboratory conditions, the vagrant shrew can detect a 16 cm^2 opening, from 30 cm, absent of any visual cues. Although echolocation capabilities of the vagrant shrew are far inferior to that of most bats, they likely can be used for exploration of its surroundings.

Molts occur in spring and autumn.

Reproduction: In Montana, spermatogenesis in the vagrant shrew begins in February, reaches full activity by March, and extends through late the following autumn. Breeding begins in late March and peaks in late April to early May, although individual females may produce up to 3 litters over the course of the spring–summer period. Gestation lasts 20–21 days, with young born in an extremely immature condition, with poorly formed limbs that have yet to ossify and closed eyes and ears. The nature of their fetal development is reminiscent of that observed in marsupials and has been used to suggest a closer evolutionary tie between these 2 groups. Amazingly, although offspring are born in such an undeveloped state, they quickly mature and attain near adult body size at weaning 20 days after birth.

Status: Common in the western part of the state.

Gillihan, S., and K. R. Foresman. 2001. *Sorex vagrans.* Mammalian Species *In Press.*

ORDER CHIROPTERA—BATS

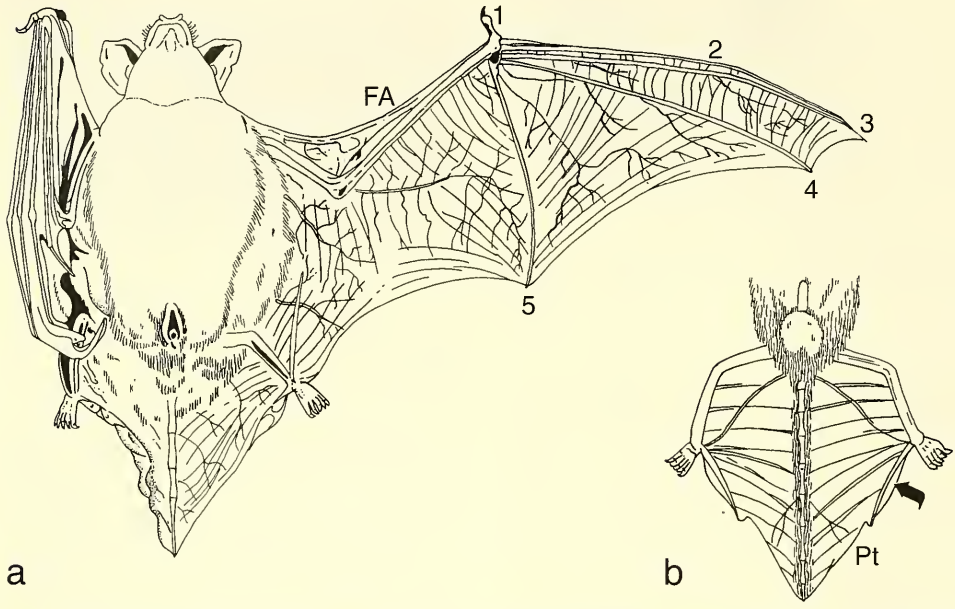


Fig. 24. Anatomy of the bat: a) appearance of an adult female showing digits (numbered, 1 = thumb), and measurement of forearm length (FA) and b) appearance of adult, sexually mature male (tail membrane, "pterygium"—Pt, and keeled calcar, arrow).

The order Chiroptera, which encompasses the bats, is 2nd only to the order Rodentia in the number of recognized species: 986, worldwide. Worldwide, this order comprises 18 families, containing 186 genera. In Montana, 15 species occur, most of which are transitory, summer residents, migrating southward in winter. The term "Chiroptera," from the Greek combination cheir, meaning "hand," and pteron, meaning "wing," refers to the skeletal support provided for the wing by the bones of the forelimb (Fig. 24). Members of this order are the only mammals to truly fly; other species such as the "flying" squirrel, order Rodentia, actually glide during a free fall. This unique ability to fly opened a new environment, the skies, into which the bats could evolve, and they have taken advantage of this niche, although most species restrict their activity to night.

Numerous anatomical and physiological specializations set bats apart from other mammals. Among these are a rotated hindlimb, that allows the hind legs to swing forward when knees are bent. This adaptation provides support for the wing membrane in the caudal region (the pterygium) and allows bats to scoop up insects while flying, trapping them in a pocket formed from this membrane (a structure resembling a baseball catcher's mitt; Fig. 24b). Other adaptations include highly specialized ears, nostrils, and vocal cords and neurological modifications which, when used together to produce and analyze ultrasounds, provide the bat with extremely sophisticated echolocation capabilities.

The term echolocation refers to the ability to use emitted soundwaves and their echoes as a means of locating objects in the environment. Other mammalian species

have evolved this capability, including porpoises, whales, and some shrews. Bats, however, are the acknowledged masters. A sophisticated pattern of soundwaves generated by the vocal cords is emitted into the environment, either through the mouth or nostrils. As these soundwaves contact objects, such as vegetation or potential food (e.g., flying insects), they rebound, producing an echo (a returning soundwave). The original soundwaves are modified by their contact with these objects and return to the animal. Using highly modified ears, bats are able to capture and transmit these signals to the brain. Species which use echolocation have brain centers that can compare the echo to the original sound emitted and account for the time-lag between emission of the original signal and reception of the echo. In this manner, the animal is able to determine how large an object is (from which the signal bounced), how far away it is, and whether or not it is moving and if so, in what direction (the latter information is obtained by comparing a series of emitted signals and their companion echoes). The level of sophistication of this echolocation ability is truly amazing. Some bats in the Suborder Microchiroptera (which includes all of Montana's species) are able to discriminate objects as small as 4.8 mm from distances exceeding 2.9 m (Suthers and Wenstrup 1987). Radar, which humans use to track airplanes, is crude compared with echolocation capabilities of most bats.

Most species of bats produce soundwaves at frequencies that are higher (>20 kHz) than those within the hearing range of humans. By convention, they are referred to as ultrasounds. This is why, when you observe bats fluttering overhead, they appear to be quiet. In reality, the noise is very loud; bats are not only producing sounds above our hearing capabilities, but they are producing these sounds at decibel levels comparable to a jet at takeoff. Fortunately, our ears are incapable of hearing these higher frequency sounds. With proper electronic equipment (commonly called bat detectors), we can discern these sounds. Each species of bat produces a distinctive pattern of calls from which it can be identified (Fenton and Bell 1981). The frequency and duration of these calls, for the bats found in Montana, are summarized below:

Diagnostic soundwave patterns used by Montana bats during echolocation (Barclay 1984; Fenton and Bell 1981; Obrist and Wenstrup 1998; van Zyll de Jong 1984).

Species	Frequency (kHz)	Duration (msec)	Harmonics (*n*)
Antrozous pallidus	49–26	5	2
Corynorhinus townsendii	50–20	5	—
Eptesicus fuscus	48–27	10	3
Euderma maculatum	14–6	5	2
Lasionycteris noctivagans	35–25	10	—
Lasiurus borealis	75–40	6	—
Lasiurus cinereus	39–26	15	2
Myotis californicus	67–37	6	2
Myotis ciliolabrum	55–41	5	—
Myotis evotis	97–54	5	none
Myotis keenii	110–38	5	—
Myotis lucifugus	80–40	5	2, 3
Myotis thysanodes	49–31	8	—
Myotis volans	89–40	10	3
Myotis yumanensis	80–40	5	—

Bat species in Montana range from 3 g to about 35 g; from common year-round resident species, such as the little brown myotis (*Myotis lucifugus*) to rare migratory species, such as the red bat (*Lasiurus borealis*) and spotted bat (*Euderma maculatum*). With the exception of the pallid bat, all of these species are strictly insectivorous.

Although bats are beneficial in controlling insects, particularly bothersome species such as mosquitoes, they have been associated perceptually with transmission of rabies. However, occurrence of rabies in bat populations is <1% (Trimarchi and Debbie 1977). Although no scientific screening studies have been conducted on the incidence of rabies in bat populations in Montana, <1 bat/year turned in to the author has tested positive for this disease.

Pelage characteristics used to identify bats are often subtle, making identification of living individuals difficult. Identification of museum specimens also may be confusing

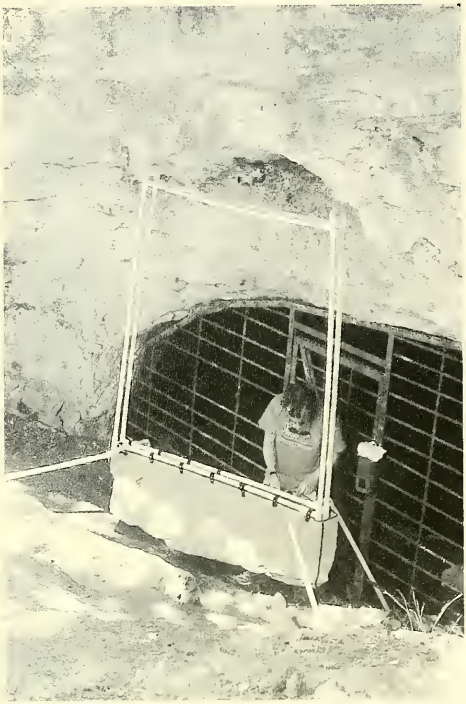


Fig. 25. Harp trap set in front of Mystery Cave in the Pryor Mountains of southcentral Montana.

because many of the required measurements of the forelimb, hind foot, or ear, taken when the animal was obtained, can change as these structures may shrink during drying. This becomes particularly apparent in the genus *Myotis*. The keel, formed from a flap of skin attached to the calcar, a bony projection from the calcaneus bone of the hind foot, may be difficult to detect if the specimen was not pinned out during museum preparation.

Family Vespertilionidae—Vespertilionid Bats*

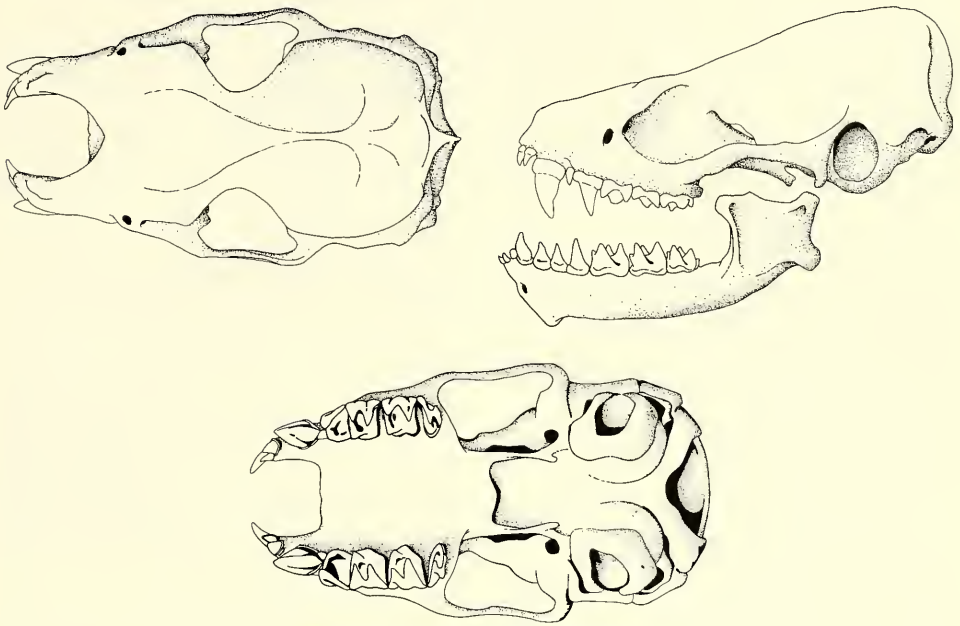


Fig. 26. Skull of a bat (*Lasionycterus*).

Pallid Bat
Antrozous pallidus

Scientific Name: The pallid bat was first described by LeConte in 1856, from a type specimen obtained in El Paso, El Paso County, Texas, and given the scientific distinction *Vespertilio pallidus.* The current designation was ascribed by Allen in 1862. The generic designation, *Antrozous,* is from the Greek combination, antron, referring to "cave," and zoos, meaning "living in." The specific epithet, *pallidus,* is Latin for "pale," which refers to its coloration.

Description: The pallid bat is 1 of the most distinctive bats found in Montana. It is large-bodied, with large ears (21–37 mm),

Pallid bat (*Antrozous pallidus*). See plate 1.

* For representative skull characteristics of this taxonomic family refer to Fig. 26.

Map 11. Distribution of the pallid bat, *Antrozous pallidus*.

and a horseshoe-shaped ridge on its muzzle. It is easily recognized by its distinctive color: dorsal fur is a creamy, yellowish-white, with a venter of white fur. Because of its distinctive color, large size, and prominent, large ears, the pallid bat should not be confused with any other bats in Montana.

Measurements: [mm(*n*)]: TL = ♂ 104.0(1)/♀ 110.0(1); Ta = ♂ 45.0(1)/♀ 42.0(1); HF = ♂ 12.0(1)/♀ 13.0(1); E = ♂ 58.0(1)/♀ 55.1(1); M [g(*n*)] = ♂ 20.5(1)/♀ 19.6(1). Dental formula: i 1/2, c 1/1, p 1/2, m 3/3, total 28.

Distribution: The pallid bat is widely distributed across the western one-third of North America, extending from British Columbia, southward, to central Mexico. It ranges from the Pacific Coast eastward to Kansas but is found only sparsely in Idaho, Wyoming, and Montana. It has only been recorded from Montana since 1980, when the 1st specimen was collected in Carbon County (Shryer and Flath 1980). Since this time, intensive collecting in the appropriate habitat has produced 24 additional individuals (also from Carbon County); lactating females and juveniles have been collected (Worthington 1991).

Ecology and Behavior: Dry, desert environments seem to be preferred, but pallid bats are known to range into oak and pine forests. It roosts in rock crevices and barns, during summer, where it clusters with other individuals. Summer studies in the Pryor Mountains of southcentral Montana failed to find this species within any of the caves monitored, but individuals were collected with mist nets over several water sources (Worthington 1991). Presence of both sexes, lactating females, and juveniles suggests that breeding may occur in this region. The pallid bat is assumed to hibernate during winter. Although no winter records of the pallid bat have been recorded in Montana, if breeding occurs here, it is probably a year-round resident.

Due to its size and rounded wing structure, the flight capabilities of the pallid bat favor feeding on large slow-moving insects, such as moths. It has adopted 2 interesting feeding modes: gleaning of insects from vegetation (predominantly cicadas, katydids, and sphingid moths) and foraging on the ground, feeding primarily on scorpions, crickets, and beetles. The pallid bat is able to land on the ground and run on its wrists, while chasing its prey. This terrestrial locomotor capability, coupled with its large solid skull and large canines, provides it with the force and mobility required for killing not only hard-bodied, ground-dwelling insects, but also small vertebrates such as the silky pocket mouse (*Perognathus flavus*) and the short-horned lizard (*Phrynosoma douglassi*). Foraging activity is concentrated around dusk and just before dawn.

The pallid bat has much greater auditory sensitivity in the lower frequency ranges (5–15 kHz) than most species of bats. This appears to coincide with the sound patterns produced by insects rustling on the ground.

Reproduction: Testicular development in males begins early in summer; breeding commences in October and is thought to extend through February. As with other Montana bats, females store sperm until the following spring when ovulation and fertilization occur (a phenomenon known as "delayed fertilization"). Delayed development is suspected because the timing of parturition varies depending upon local environmental temperatures.

Two young are born between May and June and are weaned 6–8 weeks later.

Status: Rare. Only 25 individuals have been captured in Carbon County.

Hermanson, J. W., and T. J. O'Shea. 1983. *Antrozous pallidus.* Mammalian Species 213:1–8.

Townsend's Big-Eared Bat
Corynorhinus townsendii

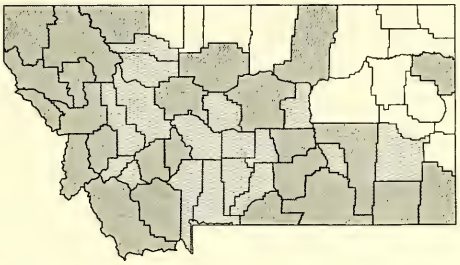
Townsend's big-eared bat (*Corynorhinus townsendii*).

Scientific Name: Townsend's big-eared bat was first described by Cooper in 1837, from a type specimen thought to be collected at Fort Vancouver, Clark County, Washington, and it is 1 of the most unique bat species in Montana. The generic designation, *Corynorhinus,* comes from the Greek combination koryne, which means "club-shaped bud," and rhinos, which refers to nose; together they describe the large, glandular bulbs between the nostrils and eyes. The specific epithet is in honor of the naturalist Charles H. Townsend. Until recently, this species was placed in the genus *Plecotus,* and some authors still use this designation.

Description: Presence of extremely large ears (30–39 mm in length) sets this species apart from all other Montana bats, with the exception of the spotted and pallid bats. The latter 2 species easily are separated by their distinctive pelages. Townsend's big-eared bat is a medium-sized species, with a wingspan of 30 cm. Dorsal fur is slate in color, tipped with brown; ventral hairs are a lighter shade of brown.

Measurements: [mm(*n*)]: TL = ♂ 95.7(10)/♀ 96.7(3); Ta = ♂ 45.5(10)/♀ 48.0(3); HF = ♂ 10.3(10)/♀ 10.7(3); E = ♂ 35.5(8)/♀ 29.5(2); M [g(*n*)] = ♂ 9.3(10)/♀ 9.2(7). Dental formula: i 2/3, c 1/1, p 2/3, m 3/3, total 36.

Distribution: The Townsend's big-eared bat extends from British Columbia across the western half of the United States southward through central Mexico. Isolated populations exist in Oklahoma, Arkansas, Missouri, Kentucky, and the Virginias. This is 1 of the rarest species in Montana and is currently listed as a species of special concern by the United States Forest Service. Until recently, only 1 resident population was known in the cave system at Lewis and Clark Caverns in Jefferson County. Other populations have since been discovered, among which are those in abandoned coal mines in the Bull Mountains of Musselshell County (Swenson 1970) and a small population (~75) found in a private abandoned mine shaft in Missoula County in 1989. However, specimens have been collected from numerous locations in the state (Lampe et al. 1974, Swenson and Shanks 1979). Records from southeastern Montana are not surprising because the largest



Map 12. Distribution of Townsend's big-eared bat, *Corynorhinus townsendii.*

known colony thought to exist in the United States is located in Jewel Cave near Rapid City, South Dakota.

Ecology and Behavior: In general the big-eared bat prefers to roost alone or in small clusters in cold caves and mine shafts. This is only 1 of 3 bat species known to overwinter in the state. It hangs exposed from the cave ceiling, rather than hiding in cracks and crevices, and is thus susceptible to disturbance when hibernating. After disturbed, it will frequently abandon its roost, greatly increasing its chances of death. Wing banding appears to be particularly deleterious to this species.

A wide variety of habitats are used by big-eared bats throughout its range. In Montana, it is found from western mesic Douglas-fir forests to the more arid Rocky Mountain juniper–limber pine–curl leaf mountain mahogany vegetative type. Localities surrounding Lewis and Clark Caverns have a predominance of big sage–silver sage sagebrush understory, and localities in the forested part of the Pryor Mountains are characterized by Utah juniper–black sagebrush communities.

Structural morphology of the wing, with its comparatively large width-to-length ratio and rounded outer tips, produces a wing with relatively low wing loading and aspect ratios. This configuration imparts significant lifting capacity and allows this species great maneuverability. Slow flight is the rule, and the big-eared bat is able to hover when looking for food. Large ears are thought to have evolved in conjunction with echolocation capabilities and allow big-eared bats to use lower intensity sounds than many other species. Big-eared bats can readily distinguish between their own echolocation signals and background noise. This latter fact, coupled with the capability of hovering flight, may permit this species to glean insects off vegetation.

Small moths (order Lepidoptera) are the preferred food, although other insects (Coleoptera, Diptera, and Hymenoptera) have been recorded. Most foraging activity occurs late at night.

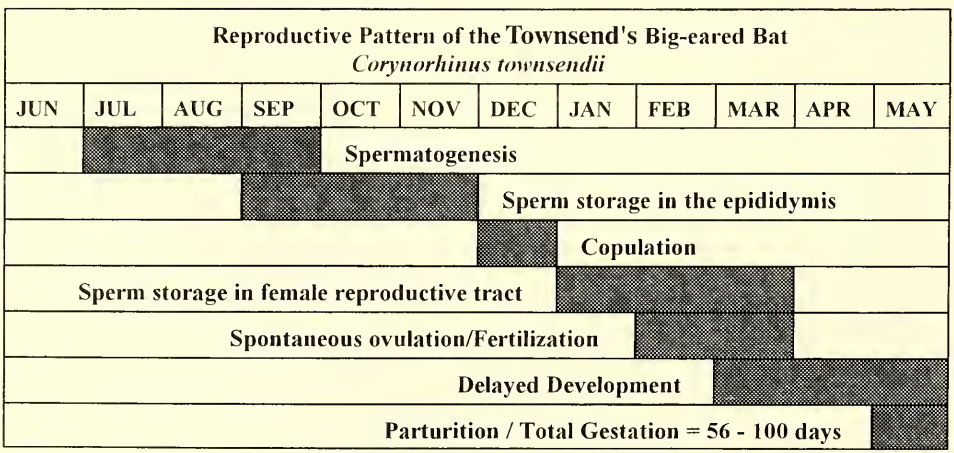


Fig. 27. Reproductive patterns in male and female Townsend's big-eared bats.

Reproduction: The Townsend's big-eared bat exhibits 2 interesting reproductive strategies: delayed fertilization and delayed development (Fig. 27). Breeding begins in autumn and likely continues through February, after females enter hibernacula. Sperm storage occurs, with fertilization delayed until spring. After conception occurs, development of the fetus is influenced by maternal body temperature. If spring temperatures are cool and the female is forced to enter torpor frequently, embryonic and fetal development will slow, which extends gestation. Pregnancies can range from 56 to 100 days in length, with 1 young born in late spring to early summer.

The male reproductive cycle is also unique (Fig. 27). Spermatogenesis begins in late summer and peaks in September, at which time testicular regression occurs. Sperm are stored in the epididymides up to several months before copulation.

Status: Rare, occurring in isolated populations.

Kunz, T. H., and R. A. Martin. 1982. *Plecotus townsendii.* Mammalian Species 175:1–6.

Big Brown Bat
Eptesicus fuscus

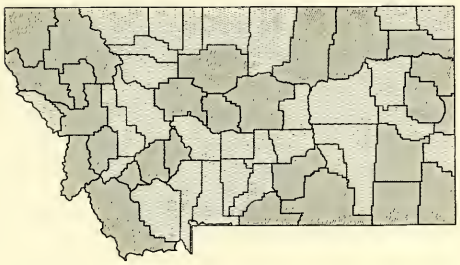
Big brown bat (Eptesicus fuscus). See plate 2.

Scientific Name: The big brown bat was first described under the name of *Vespertilio fuscus* by Palisot de Beauvois, in 1796, from the type locality of Philadelphia, Pennsylvania. First use of the current name combination, *Eptesicus fuscus,* was made by Mehely, in 1900. Rafinesque coined the generic name in 1820 which he drew from the Greek words epien, meaning "to fly," and oikos, which means "home"; thus "house flyer." The specific epithet, *fuscus,* is Latin for "brown" or "dusky."

Description: As the vernacular name implies, the big brown bat is large and dark brown in color (it is the largest brown-colored bat in North America). The dorsal surface blends into a lighter brown venter. It has short rounded ears and long (38 cm) broad wings. The big brown bat could, at first glance, be easily confused with any of the *Myotis* species in the state. It is, however, at least 2–3 times larger than those species.

Measurements: [mm(*n*)]: TL = ♂ 101.5(4)/♀ 111.5(2); Ta = ♂ 44.0(4)/♀ 42(2); HF = ♂ 13(3)/♀ 13(2); E = ♂ 14.3(4)/♀ 16.0(1); M [g(*n*)] = ♂ 12.8(4)/♀ 17.0(2). Dental formula: i 2/3, c 1/1, p 1/2, m 3/3, total 32.

Distribution: The big brown bat is 1 of the most widely distributed bat species in North America. Its distribution extends across the continental United States and the southern regions of all bordering Canadian provinces, southward throughout Central America, with projections into northwestern South America. It is a common resident of Montana, although it is not found often in large numbers. Maternity colonies are known in the state (Swenson and Shanks 1979).



Map 13. Distribution of the big brown bat, *Eptesicus fuscus.*

Ecology and Behavior: The big brown bat appears to be a habitat generalist, foraging as commonly over water as over land, and using open and forested areas with significant canopy closure. Foraging begins about 1 hour after sunset, peaking soon thereafter, although activity may continue throughout the night. Small flying beetles (order Coleoptera) make up the most significant component of the diet, although true bugs (Hemiptera), flying ants (Hymenoptera) and moths (Lepidoptera) are eaten in abundance.

Males precede females into hibernacula in late autumn. Typically mines, caves, and barns are used for this purpose. In warmer regions, both sexes may leave hibernacula in winter. Maternity colonies form in barns and houses following hibernation. Males may roost as solitary individuals, with females following parturition, or in all-male colonies during summer. Individuals can live as long as 19 years in the wild.

Because the big brown bat is common throughout the country, long-lived, and easily raised in captivity, it has been the focus of a great deal of physiological and behavioral research (Kurta and Baker 1990). As is typical of species that hibernate, the big brown bat can lower its resting heart rate from 450 beats/min (bpm) at 37°C to 4 bpm at 5°C. When it takes flight, heart rate climbs to >1,000 bpm.

Echolocation calls used by the big brown bat fall in the lower to middle range of other Montana species, with a frequency of 27–48 kHz. Its maximum acoustic sensitivity is broad (10–45 kHz), and it can hear loud sounds at frequencies as low as 0.5 kHz, allowing it to hear many insects in flight.

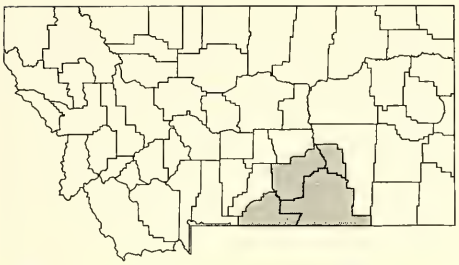
Reproduction: Males begin testicular development and spermatogenesis in late summer. Testicular regression and sperm storage in the epididymis occur in September. Copulation can occur anytime from September to March, with sperm storage occurring in the reproductive tract of females until spring. Ovulation and fertilization occur in early spring, followed by a gestation of 60 days. Gestation length may be extended if the female enters prolonged periods of torpor. One young is born between May and July. Juveniles can fly at 18–35 days of age, with males reaching sexual maturity during their 1st autumn. Some, but not all, females breed during their 1st year.

Status: Common.

Kurta, A., and R. H. Baker. 1990. *Eptesicus fuscus.* Mammalian Species 356:1–10.

Spotted Bat
Euderma maculatum

Scientific Name: The spotted bat was first described as *Histitus maculatus* by Allen in 1892 and has been recognized by that name since 1894. The type locality for this species is the Santa Clara Valley in Los Angeles County, California. The generic name, *Euderma,* is of Greek origin, a combination of the words Eu, meaning "good," and derm, meaning "skin." The specific epithet, *maculatum,* is from the Latin, macula, which means "spot or mark."



Map 14. Distribution of the spotted bat, *Euderma maculatum*.

Description: The striking spotted pelage of the spotted bat sets it apart from all other North American bats. There are 3 large white spots, 1 just below each shoulder and 1 near the rump, forming a triangular pattern against a dark black background. This pattern, coupled with extremely large, naked, pink ears (measuring 45–50 mm), and a large tragus (a fleshy projection at the base of the ear), make its identification undeniable. It also is 1 of the largest bats in Montana (15–17 g).

Measurements: [mm(*n*); Warner 1981]: TL = ♂/♀ 107–115; MT ♂ 114.0(1)/♀ 132.0(1); Ta = ♂/♀ 47–50; MT ♂ 48.0(1)/♀ 58.0(1); HF = MT ♂ 9.0(1)/♀ 12.0(1); E = ♂/♀ 45–50; MT ♂ 39.0(1)/♀ 39.0(1); M [g(*n*)] = ♂ none/MT ♂ 16.0(1). Dental formula: i 2/3, c 1/1, p 2/2, m 3/3, total 34.

Distribution: The range of the spotted bat extends from Montana, directly southward through Idaho and Wyoming, as far as central Mexico. Only 3 records exist in Montana, fewer than any other mammal in the state. A single, subadult male was captured in Billings (Yellowstone County) in 1949, after flying into a house (Nicholoson 1950). Two additional individuals, a lactating adult and a juvenile female, were caught in 1990 after 2 months of intensive comprehensive studies in the Pryor Mountains, Carbon County (Worthington 1991). Additional individuals were heard at several localities throughout the Bighorn Canyon National Recreation Area by Worthington (1991) and this author in 1990. This region contains prime habitat for this species, and presence of a lactating female suggests that breeding may occur in the area. The low rate of capture may be a reflection of the spotted bat's preference for rough, dry, desert habitat and reduced trapping effort in such areas. The spotted bat forages at higher altitudes and thus avoids mist nets. Regardless, it is considered 1 of the rarest mammals in the state, if not the United States.

Ecology and Behavior: The spotted bat frequents a wide range of habitats from montane forests to, most commonly, desolate deserts (Leonard and Fenton 1983; Wai-Ping and Fenton 1989). Available roosting sites dictate its presence more than the habitat over which to forage. Cliffs and steep canyon walls are preferred roost localities. This may, in part, account for its presence in the Bighorn Canyon region of southcentral Montana.

Foraging begins at dusk and continues throughout the night (Leonard and Fenton 1983; Wai-Ping and Fenton 1989). Diet consists almost entirely of noctuid moths and June beetles. Echolocation calls produced by the spotted bat are among the lowest in frequency of any North American species, ranging from 8–15 kHz (Leonard and Fenton 1984; Woodsworth et al. 1981). These calls are audible to the human ear, making identification on the wing relatively easy.

The spotted bat readily enters torpor as ambient temperatures decrease. The extremely large ears, which help in evaporative cooling of the animal under warm conditions, become a liability as the environment cools. To compensate for this problem, the spotted bat rolls its ears up as it enters torpor, thereby decreasing the evaporative surface area.

Reproduction: Little information is available on the reproductive biology of this species. Breeding probably occurs in mid-to-late autumn, as in other vespertilionids.

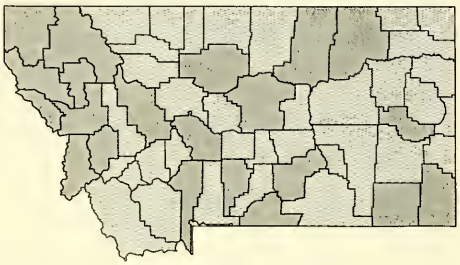
Parturition has been observed in early June in 3 individuals (Warner 1981), each of which gave birth to 1 young.

Status: Rare.

Watkins, L. C. 1977. *Euderma maculatum.* Mammalian Species 77:1–4.

Silver-haired Bat
Lasionycteris noctivagans

Scientific Name: The silver-haired bat was first described by LeConte in 1831, as a member of the genus *Vespertilio,* from a type locality of the eastern United States. In 1865, it was recognized as belonging to a separate genus, based largely on dental differences. Generic designation, *Lasionycteris,* comes from the compounded Greek words lasios, meaning "hairy," and nycteris, meaning "bat." The specific epithet is of Latin origin from the words noctis, meaning "night," and vagrans, meaning "wandering."



Map 15. Distribution of the silver-haired bat, *Lasionycteris noctivagans.*

Description: The silver-haired bat is medium-sized with a wingspan of 30 cm. The frosty appearance, produced by the silver tipping of the dark brown to black dorsal hairs (and the basis for its vernacular name) makes it easily identifiable. The membrane running between the hind legs and tail also is distinctively furred on the dorsal basal half. Ears are black, naked, and rounded. Due to its distinctive color, the silver-haired bat should not be confused with other bats in Montana.

Measurements: [mm(*n*)]: TL = ♂ 88.6(5)/♀ 98.8(6); Ta = ♂ 34.8(5)/♀ 40.3(6); HF = ♂ 9.8(2)/♀ 9.8(4); E = ♂ 12.5(4)/♀ 16.3(4); M [g(*n*)] = ♂ 8.3(5)/♀ 12.1(4). Dental formula: i 2/2, c 1/1, p 2/3, m 3/3, total 34.

Distribution: The silver-haired bat is common throughout North America extending from Alaska across all of the southern Canadian provinces and the continental United States, southward into northeastern Mexico. It is 1 of the more common migratory species in Montana. A majority of Montana records have come from western counties, although 43 were taken in Carter County (Swenson and Bent 1977; Worthington 1991).

Ecology and Behavior: The silver-haired bat likely prefers a solitary existence, roosting in trees during summer; it has not yet been found in caves or mine shafts in the state. Winter-roosting records show this species to inhabit caves, mine shafts, and houses.

This medium-sized bat (8–11 g) is a slow flier and an opportunistic feeder. It typically feeds later than most species in a bimodal fashion, first 2–4 hours after sunset, and then 6–8 hours after sunset. Foraging occurs over ponds and waterways, in or near the edge of coniferous forests. A wide range of insect species have been recorded in the diet of specimens from Montana, specifically in the orders Hemiptera, Lepidoptera, Coleoptera, Diptera, and Trichoptera (Jones et al. 1973).

The oldest recorded individual lived 12 years; average life expectancy is unknown.

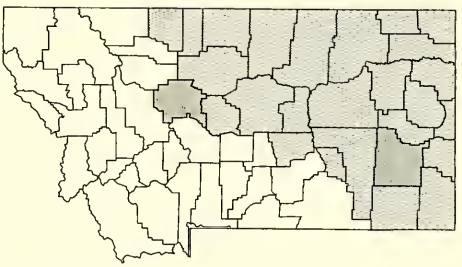
Reproduction: As with many vespertilionid bats, the silver-haired bat is thought to breed in autumn, with females storing sperm in their reproductive tract for later fertilization in April or May. Litter size is 2, following a gestation period of 50–60 days. Volant young and adult lactating females have been taken in southeastern Montana in mid-July (Jones et al. 1973). Sexual maturity in both sexes can be reached during their 1st summer.

Status: Common, but infrequent.

Kunz, T. H. 1982. *Lasionycteris noctivagans.* Mammalian Species 172:1–5.

Red Bat
Lasiurus borealis

Scientific Name: The red bat was first described in 1776 from a type specimen collected in New York by P. L. S. Müller. Originally described as *Vespertilio borealis,* the genus designation *Lasiurus* was proposed by J. E. Gray in 1831 and is used today. The genus name is from the Greek, lasios, meaning "shaggy or hairy;" *borealis* is from Latin meaning "northern."



Map 16. Distribution of the red bat, *Lasiurus borealis.*

Description: The red bat is quite distinctive as its name suggests. In coloration, it ranges from brick red or bright orange to yellowish-brown across its back mixed with white hairs. Darker hairs commonly are tipped in white giving a frosted appearance. The ventral surface is lighter in color and shoulders often possess a buffy white patch. One distinguishing characteristic easily observed with a specimen in hand is the well-furred interfemoral membrane (skin connecting the hindlimbs and within which the tail lies). Ears are rounded and broad, and wings are relatively long and pointed. The red bat can not be confused with any other bat in the state due to its highly distinctive coloration.

Measurements: [mm(*n*); Shump and Shump 1980]: TL = ♂ 102.7(12)/♀ 107(1); Ta = ♂ 43.2(9)/♀ 49(1); HF = ♂ 7.9(12)/♀ 7.0(1); E = ♂ 10.6(6)/♀ 9(1); M [g(*n*)] = ♂ 10.6(5)/♀ no measurement. Dental formula: i 1/3, c 1/1, p 2/2, m 3/3, total 32.

Distribution: The red bat is found from southern Canada southward throughout the continental United States, Mexico, Central America, and most of South America. It is definitely a migratory species in Montana, with its existence in the state only recently being verified (Lemke 1999). Only 2 specimens have been collected, the 1st in September 1997 in the southeastern part of Montana near Ismay (Custer County), and the 2nd in September 1998 in northcentral Montana near Big Sandy (Chouteau County). The only other record in Montana was collected in the 1880s "on the Yellowstone," but no additional information was provided and thus verification is impossible. Probably both individuals were migrating southward across the state when captured.

Ecology and Behavior: Red bats are a solitary, foliage-roosting species similar to hoary bats, roosting most often along forest edges. In the midwest, roosting sites were, on

average, 2 m above ground. In Illinois, several individuals have been described using the underside of sunflower leaves 2.3 m from the ground. The same leaf was used independently by an adult male, female, and a juvenile male even although numerous other sites were readily available, suggesting that some form of communication was occurring. Many bat species use night roosts during summer, which are often situated near foraging areas; bats retreat to diurnal roost sites during the day. This behavior may occur in red bats although, it is difficult to determine because of their solitary nature.

Foraging occurs 1–2 hours after sunset, and red bats concentrate on large insects such as moths, crickets, beetles, and bugs. Much feeding activity occurs at tree-top level; red bats also are commonly observed foraging around street lights or flood lights on outbuildings (Hickey et al. 1996). Timing of feeding activity may be influenced by temporal activity of preferred prey items. In the Midwest, a temporal partitioning in the foraging pattern of several species has been found, with red bats foraging first, followed by the silver-haired bat and then the hoary bat. Although Hickey et al. (1996) found no such temporal overlap, they did observe partitioning of insects by size; the hoary bat consistently ate larger-sized moths while the red bat ate smaller moths.

The red bat, although in the same genus as the hoary bat, is only one-half the size. Their wing conformations are similar—long and narrow and built for a fast, somewhat straight flight pattern, but because red bats are smaller (wings 29–32 cm), they have more maneuverability.

Red bats are highly migratory. With so few records of this species in Montana, however, no information exists on the time of arrival or exit from the state. They probably arrive in Montana in May and depart in September. Red bats may just travel through Montana to summer in British Columbia and Alberta, although they are just as uncommon in those Canadian provinces. In the midwestern and southeastern parts of the United States males and females occupy different summer ranges and migrate at different times (Barclay 1984).

In the late autumn and winter, red bats hibernate as do all of Montana's bat species. Rather than occupy caves such as *Myotis,* red bats continue to roost in trees. Torpor may be entered whenever temperature falls below 20°C, but they have been observed flying during much cooler temperatures (13°C). Body temperature will drop to just above freezing and if ambient temperatures continue to decrease, the bats will increase their metabolic activity to maintain this core temperature. Populations which overwinter in more southern regions may only periodically hibernate; at other times they will feed throughout these months on moths and flies (Whitaker et al. 1997). Because the red bat continues to roost in more exposed areas rather than retreat to warmer caves, it has numerous anatomical features that provide additional insulation and reduce heat loss: well furred body, a densely furred pterygium that can be pulled over its body much like a quilt, and small rounded ears.

Although the red bat exhibits 1 of the higher incidences of rabies for bat species in the southeastern and mid-Atlantic regions of the United States (Krebs et al. 1995), both individuals captured in Montana tested negative for this disease.

Reproduction: No reproductive information is available for this species in Montana. In the midwest where the red bat is common, breeding occurs in August and September. As with other vespertilionids, the red bat exhibits delayed fertilization at this time. The female ovulates in spring at which time conception occurs and pregnancy begins. Gestation has been estimated at 80–90 days with young born in early June. Litter size is 1–5 young with a mean of 2.3. Lactation lasts 38 days, and young are weaned at 4–6 weeks.

Status: Rare. Only 2 specimens recently have been verified in Montana.

Shump, K. A., and A. U. Shump. 1982. *Lasiurus borealis.* Mammalian Species 183:1–6.

Hoary Bat
Lasiurus cinereus

Hoary bat (*Lasiurus cinereus*). See plate 2.

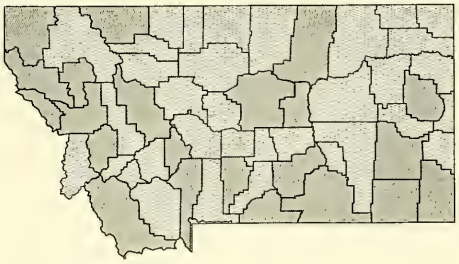
Scientific Name: The hoary bat was first described in 1796 from a type specimen collected in Philadelphia, Pennsylvania. The present taxonomic distinction was provided by Allen (1864), in a revision of the bats of North America. The genus name, *Lasiurus,* is from the Greek, lasios, meaning "shaggy or hairy," and urus, meaning "tail," while the specific epithet *cinereus,* is Latin, meaning "ash-colored," a reference to its pelage coloration.

Description: This is the largest bat in Montana and 1 of the largest in the United States, with a wingspan of about 41 cm. Its grizzled (hoary) coat, from which it gets its vernacular name, also makes it 1 of the easiest to identify. Ears are more robust than in most species: short and rounded in confirmation with a distinctive black hair edging. Due to its size, color, distinctive facial features, and flight characteristics, the hoary bat should not be confused with any other bat in the state.

Measurements: [mm(*n*)]: TL = ♂ 130.0(1)/♀ 134.0(1); Ta = ♂ 65.0(1)/♀ 50.0(1); HF = ♂ 11.0(1)/♀ 10.0(1); E = ♂ 15.0(1)/♀ 11.0(1); M [g(n)] = ♂ 19.3(1)/♀ 19.5(1). Dental formula: i 1/3, c 1/1, p 2/2, m 3/3, total 32.

Distribution: The hoary bat is found throughout North America southeast of Alaska, extending into Mexico, parts of South America, and Hawaii, making it the most widespread vespertilionid species in North America. It is a migratory species in Montana, appearing in May for summer and presumably moving southward in September. Although it likely segregates by sex during migration, with females moving into the northcentral and northeastern United States and males moving into the western United States both sexes come to Montana in summer (Jones et al. 1973; Swenson and Shanks 1979; Worthington 1991). Additionally, lactating females and young occur in southeastern Montana (Lampe et al. 1974; Swenson and Shanks 1979; Worthington 1991). No individuals have, as yet, been found overwintering in Montana, and no information is available on where they migrate. Few records of the hoary bat are deposited in the University of Montana Museum, although 2 summers of intensive collecting in the Pryor Mountains (Big Horn County) produced 22 individuals (Worthington 1991). Other records have been recorded around the state.

Ecology and Behavior: Hoary bats are solitary and roost on foliage in Montana; thus, they are not often observed. In Oregon, it is known to prefer old-growth (>200 year old) Douglas fir–western hemlock forests (Perkins and Cross 1988), likely due to availability of roost sites. As such,



Map 17. Distribution of the hoary bat, *Lasiurus cinereus.*

loss of old-growth stands in the Northwest is viewed as a potential threat to this species' viability. Height of the roosting sites in the tree canopy varies from 3–12 m above ground, depending on sex of the individual, and whether or not young are present. Adult males roost lower in the canopy, while females, particularly those with young, roost much higher. The dense fur that covers their body and pterygium likely has significant insulating capabilities. The pterygium is often pulled over the body to provide added insulative protection (Shump and Shump 1980). The larger size and dense pelage allows hoary bats to forage at ambient temperatures as low as 0°C.

The size and wing confirmation of these bats are conducive to a fast, straight flight, making them easy to identify on the wing. They are 1 of the fastest bat species in North America. Thus, they tend to forage more efficiently over open uncluttered spaces for large insect species. Foraging may occur over water, as with most smaller species, but the hoary bat most commonly forages along roads, forest edges, and clearings within the forest (Barclay 1985). It feeds later in the evening than most other species in Montana, emerging about 1 hour after sunset. Hoary bats in Montana feed upon scarab beetles (order Coleoptera), a variety of moths (Lepidoptera), true bugs (Hemiptera), and other insects (Jones et al. 1973).

Reproduction: Breeding occurs in early autumn; the exact time depends on latitude. Following the delay in fertilization, which lasts through winter, gestation is 90 days; lactating females have been collected in Montana in mid-July. Young are born in day roosts where they also are raised. At birth, they are covered with a fine layer of silver-gray hair; their eyes and ears are closed. Development proceeds rapidly, and they are capable of flight by 33 days postparturition. This is the only species of bat that has >2 young; litter sizes of 4 are not unusual.

Status: Locally common but never abundant.

Shump, K. A., and A. U. Shump. 1982. *Lasiurus cinereus.* Mammalian Species 185:1–5.

California Myotis
Myotis californicus

Scientific Name: The California myotis was initially described as *Vespertilio californicus* by John James Audubon, the famous American ornithologist, and his close friend John Bachman, a minister, in 1842, from type specimens collected in Monterey, California. The species was redescribed as belonging to the genus *Myotis,* in 1897, by Miller (1897). The generic designation arises from the Greek generative combination, myos, referring to "mouse," and otos, which means "of the ear," "mouse-eared." The specific epithet, *californicus,* refers to the type locality from which it was originally described.

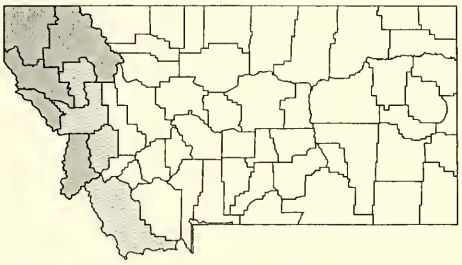
Description: The California myotis is small, dark brown to reddish-brown in body color, with black wings and ears. Wingspan is short, about 23 cm in length, and feet are small. Several of the *Myotis* species in Montana are difficult to distinguish

unless one has experience with this group. The California myotis is no exception. This species is a member of the *leibii* group, and as such has small feet, a short snout, and distinguishing skull features. In hand, it can be distinguished from the western small-footed myotis by the distribution of hair covering the snout, when viewed from above. In the California myotis, length of the snout, which is naked, is as long as the width of the nostrils, while in the western small-footed myotis it is nearly 50% longer (van Zyll de Jong 1985). In most respects, it is similar to the long-legged myotis, but foot length can be used here for separation (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 81.5(2)/♀ 79.0(1); Ta = ♂ 34.5(2)/♀ 34.0(1); HF = ♂ 6.5(2)/♀ 6.5(1); E = ♂ 14.3(2)/♀ 14.0(1); M [g(*n*)] = ♂ 5.0(2)/♀ 4.7(1). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The California myotis extends from Alaska southward along the Pacific Coast throughout Mexico. Its eastward extension brings it to Montana, Colorado, New Mexico, and Texas. Fewer than 20 individuals have been collected in Montana. Because this is such a difficult group, it is possible that additional specimens may have been handled but misidentified.

Ecology and Behavior: In the northern extension of its range, the California myotis likely inhabits forested areas, particularly those with old-growth characteristics (Thomas and West 1991). Summer roost sites consist of buildings, caves, mines, under the bark of trees, and snags. Maternity roosts and hibernacula are in the more protected buildings, caves, and mines (Christy and West 1993).



Map 18. Distribution of the California myotis, *Myotis californicus.*

As with other *Myotis,* the California myotis feeds on small flying insects, particularly moths (order Lepidoptera), true bugs (Hemiptera), beetles (Coleoptera), and flies and mosquitoes (Diptera). Much of our information on this species comes from Woodsworth (1981), from which the following description is derived. Most feeding occurs over water or around the tree canopy. Flight characteristics are similar to those of the more common little brown bat, flying slowly, low over the ground, and changing course abruptly. Most foraging bouts recorded in British Columbia (and thus more likely to represent the Montana populations) occurred just after sunset, with a 2nd period of activity between 0100 and 0200 hours.

Reproduction: Breeding information for the California myotis is consistent with other members of the genus. See the discussion for reproduction in the little brown bat, *Myotis lucifugus.* The California myotis is known to have lived to 15 years although, on average, the lifespan would be shorter.

Status: Rare. Montana is the northeastern-most extension of its range.

Simpson, M. R. 1993. *Myotis californicus.* Mammalian Species 428:1–4.

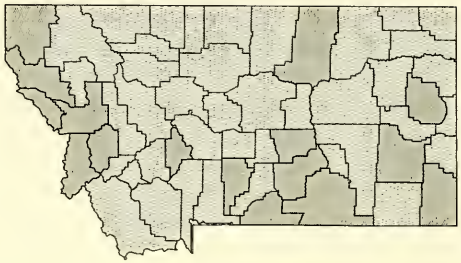
Western Small-footed Myotis
Myotis ciliolabrum

Scientific Name: The western small-footed Myotis was first described as a species in 1823 by Major Stephen H. Long (1823), in an account of an expedition from Pittsburgh to the Rocky Mountains. It was then identified as *Vespertilio subulatus* from a type specimen collected in Colorado. Several taxonomic changes occurred over the years. This species was recognized as *Myotis subulatus* until the early 1980s and then as *M. leibii,* until van Zyll de Jong (1984) and Herd (1987) showed that eastern and western populations of the small-footed myotis function as distinct species and should be regarded as such. Thus, the western species, which includes populations in Montana, is now identified as *M. ciliolabrum,* and the eastern species retains the designation *M. leibii.*

The generic distinction is from the Greek combination, myos, meaning "mouse," and otos, which refers to "ear;" a description that this species has mouse ears. The specific epithet, *ciliolabrum,* is from the Latin combination, cilium, which means "hair-like process," and labrum, which means "lip."

Description: The vernacular name for the western small-footed myotis refers to its extremely small foot (<8.5 mm). It also can be distinguished by its small body size; it is the smallest bat in Montana, weighing as little as 3 gm. Its non-glossy, yellow to blondish-brown body color also distinctly identifies the species. Black ears and wing membranes, and a prominently keeled calcar (a cartilaginous projection from the ankle which supports the pterygium), in combination with the above characteristics, clearly separate this myotis from others in Montana.

Measurements: [mm(*n*)]: TL = ♂ 77.0(2)/♀ 81.0(1); Ta = ♂ 36.5(2)/♀ 36.0(1); HF = ♂ 6.25(4)/♀ 6.5(1); E = ♂ 12.1(4)/♀ 14.0(1); M [g(*n*)] = ♂ 5.25(4)/♀ 4.9(1). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.



Map 19. Distribution of the western small-footed myotis, *Myotis ciliolabrum.*

Distribution: The western small-footed myotis is distributed across a majority of the western one-half of the United States, extending northward into British Columbia, Alberta, and Saskatchewan and southward into central Mexico. The few records from Montana are spread across the state.

Ecology and Behavior: The western small-footed myotis is far less communal than other *Myotis,* preferring to roost solitarily or in small maternity colonies in buildings and under the bark of trees during the spring and summer. In South Dakota under dry warm conditions, individuals roost in rock crevices (Tuttle and Heaney 1974)—conditions that also occur in the eastern part of Montana. Caves and mine shafts are chosen as winter hibernacula. Individuals hibernated in an abandoned coal mine in Musselshell County (Swenson 1970), which supported year-round residency. However, a majority of these bats in Montana in summer probably migrate southward in autumn.

In part because of its solitary nature, less ecological information is available for this species than for other *Myotis.* Foraging activity begins just after sunset (Woodsworth

1981), with feeding occurring along cliffs and more open areas (van Zyll de Jong 1985). Food studies indicate that the western small-footed myotis is a generalist, taking a wide variety of small insects (Jones et al. 1973).

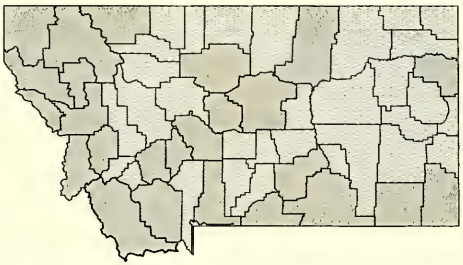
Reproduction: The western small-footed myotis exhibits the reproductive pattern typical of *Myotis*; see discussion for reproduction in the little brown bat, *Myotis lucifugus*. In Montana, a single, pregnant female was collected on 29 June (Jones et al. 1973), and 1 lactating individual was collected on 18 July (Lampe et al. 1974).

Status: Uncommon but widely distributed across the state.

Long-eared myotis
Myotis evotis

Scientific Name: Miller (1897) was the first to apply the currently accepted nomenclature to the long-eared myotis, previously identified in 1864 as *Vespertilio evotis*. Specimens for his type locality were obtained from Monterey, California. The generic designation is from the Greek genitive combination, myos, referring to "mouse," and otos, meaning "of the ear;" thus "mouse eared." The specific epithet, *evotis*, is derived from the Greek, eu, meaning "good," and otos, again referring to the "ear." This is in recognition of the longer ears characteristic of this species.

Description: This is 1 of 7 species of myotis in Montana. As the name implies these bats are small in stature, with a wingspan of about 28 cm and a weight of 5–8 g. The most apparent body characteristic that identifies the long-eared myotis in hand is its longer ears. When ears are laid forward, they extend nearly 7 mm beyond the muzzle. It is brown to light brown in color, darker on the dorsal surface than the ventral, with black ears, and black wing membranes. It also has only a slight fringe of hair edging the tail membrane. From a cursory view, the long-eared myotis appears like any other small brown bat and, as such, can be confused easily with most other *Myotis* species in Montana. Ears are clearly longer, but unless one is familiar with *Myotis*, this characteristic must be measured for positive identification.



Map 20. Distribution of the long-eared myotis, *Myotis evotis*.

Measurements: [mm(n)]: TL = ♂ 82.3(4)/♀ 89.2(6); Ta = ♂ 46.4(4)/♀ 42.0(6); HF = ♂ 8.3(9)/♀ 9.4(10); E = ♂ 18.3(8)/♀ 18.8(6); M [g(n)] = ♂ 6.5(9)/♀ 7.1(10). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The long-eared myotis extends from central British Columbia to southern Saskatchewan southward to New Mexico, Arizona, and Baja California, Mexico. A few hundred records have been obtained from Montana.

Ecology and Behavior: The long-eared myotis is found alone or in small groups, particularly in more forested regions. They are closely associated with forested stands containing old-growth characteristics (Thomas and West 1991), consistent with the western part of the state, but, where suitable roost sites exist, they occur

in many habitats. Individuals have been collected feeding over reservoirs in the short-grass prairie of southeastern Montana, adjacent to ponderosa pine-covered hills (Jones et al. 1973; Lampe et al. 1974). They also commonly inhabit caves of the Pryor Mountains (Carbon County), which are surrounded by Douglas fir forests at higher elevations, extending to more xeric conditions at lower elevations. Individuals have been taken in this region while foraging over water sources in much drier Utah-juniper–blacksage habitat as well (Worthington 1991). The long-eared myotis roosts in buildings, but it is known to use other structures such as caves, mines, trees, and rock outcroppings. Maternity colonies are found in buildings, caves, and mines. In 1977, 2 individuals hibernated in the Sidney Mine (Richland County), the 1st record of this species overwintering in Montana (Swenson and Shanks 1979). Although that observation documents residency status of the long-eared myotis in Montana, it is entirely likely that many individuals migrate from the state in autumn.

Wing structure of the long-eared myotis allows it to hover next to foliage and glean insects from the surface. Its echolocation calls provide the detailed information required at such close range in a cluttered environment (Faure and Barclay 1992). Small moths (order Lepidoptera), scarab beetles, (Coleoptera), and cicadellids have been found in stomach contents of specimens collected in Montana (Jones et al. 1973).

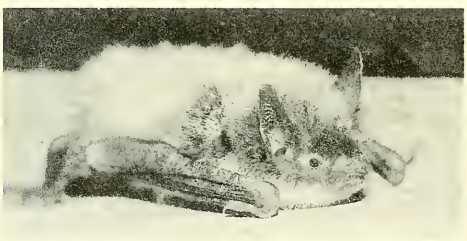
An annual molt occurs in July.

Reproduction: Little reproductive information exists for the long-eared myotis. Births have been recorded from as early as May 19th in California, but pregnant individuals are still seen in early July in Montana (Jones et al. 1973). The basic reproductive pattern is probably similar to other *Myotis* species (see the discussion for reproduction in the little brown bat, *Myotis lucifugus*).

Status: Locally abundant and widely distributed.

Manning, R. W., and J. K. Jones, Jr. 1989. *Myotis evotis*. Mammalian Species 329:1–5.

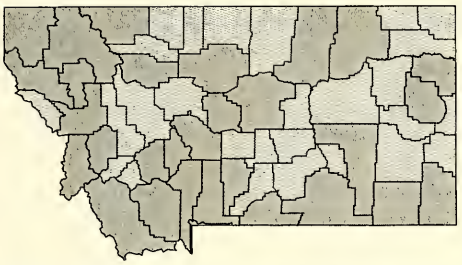
Little Brown Myotis
Myotis lucifugus



Little brown myotis (*Myotis lucifugus*).

Scientific Name: The little brown myotis was first described in 1831, under the taxonomic name of *Vespertilio lucifugus*, by John L. LeConte, a physician and naturalist, whose primary interest was butterflies and birds. The current nomenclature, *Myotis lucifugus*, was initially suggested by Miller in 1897 for specimens collected at the type locality of Sitka, Alaska. A combination of words from the Greek, myos, and otos, meaning "mouse eared" identify the genus; the specific epithet *lucifugus*, is derived from the Latin, luc, which means "light," and the verb fugio, meaning "to flee;" "light fleeing."

Description: Although the common name implies that the little brown myotis is indeed brown, color of this species actually ranges from dark brown to a light shade of brown to even yellowish. Its fur is glossy in appearance, and its ears and wing membranes are dark brown, rather than black.



Map 21. Distribution of the little brown myotis, *Myotis lucifugus.*

Another distinguishing feature is the absence of a keel on the calcar (Fig. 24). This is a small species averaging 6.5–9.5 g with a wingspan of up to 27 cm. Absence of a fringe of hair around the pterygium, and absence of a keeled calcar (Fig. 24) separates the little brown myotis from all but 1 of 7 *Myotis* species found in Montana. The glossy appearance of the dorsal hair and dark brown ear color should distinguish it from the Yuma myotis.

Measurements: [mm(*n*)]: TL = ♂ 81.7(10)/♀ 80.4(10); Ta = ♂ 59.5(10)/♀ 32.2(10); HF = ♂ 10.1(10)/♀ 9.1(10); E = ♂ 12.1(5)/♀ 12.1(10); M [g(*n*)] = ♂ 5.6(10)/♀ 5.8(10). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The little brown myotis is the most common species in Montana and possibly the entire United States. It is found throughout the continental United States (with the possible exception of Louisiana) and all Canadian provinces, with an extension into central Mexico. Although it has been recorded from only 24 of Montana's 51 counties, this is probably more a reflection of collecting efforts than occurrence. This is 1 of 3 species known to overwinter in the state, and thus, it is a permanent resident. Because of the wide distribution and abundance of the little brown myotis, it has become 1 of the most intensively studied bats.

Ecology and Behavior: During the summer, roosting occurs in a variety of structures from buildings, caves, and mines to trees, rock crevices, and snags. As such, this species is found in homes, cabins, or outbuildings, where it comes into contact with humans. It is more particular about the sites chosen for nursery roosts and hibernacula. Nursery colonies are established where ambient temperatures are warm, such as buildings, because such conditions are conducive to rapid development of the young. Hibernacula, on the other hand, are chosen based on moisture constraints and temperature. These latter sites offer protection from freezing temperatures, and provide a moisture level >90%. In suitable sites, finding several hundred bats roosting together is common. Worthington (1991), in his research on the caves of the Pryor Mountains of southcentral Montana, recorded and banded >400 male and female little brown myotis from a single cave, and I found large assemblages in barns around the state, and, in 1 case, in a church steeple.

Foraging occurs primarily over lakes and streams. A high percentage of the diet is aquatic insects, particularly chironomids, although many small insect species are taken. The little brown myotis is particularly adept at feeding through swarms of insects and may take a large number in a single feeding bout, making them perfect guests around homes and cabins, where mosquitoes are a problem. Feeding occurs from 1 to 5 m above ground as bats fly in an erratic, zig-zag fashion, chasing prey. The need to take such large numbers of prey items may reflect their relatively inefficient digestive capabilities (calculated at <70%—Barclay et al. 1991). After feeding around dusk, bats retire to night roosts where they congregate in relatively tight quarters. These night roosts differ from those chosen during the day; although the reason is unclear, this may be a function of temperature requirements for maximum energy savings.

Little brown myotis have well-developed echolocation that helps them forage on flying insects (Fig. 28). They produce sound sweeps in the range of 80–40 kHz, with 2–3 harmonics incorporated into their calls.

Fig. 28. Capture of an insect in flight by the little brown myotis.

These sounds are produced at high intensities exceeding 110 decibels.

Many anatomical and physiological studies have been conducted on the little brown myotis. Resting bats develop heart rates of about 200 bpm. This value can exceed 1,300 bpm in flight and may be reduced to 10–20 bpm during hibernation. Daily torpor may occur during spring, summer, and early autumn, whereas extended hibernation occurs during winter. Storage and rapid metabolism of specialized fats (brown fat) allows for significant heat production during these periods. Hibernation bouts as long as 90 days can occur without arousal. Although water may be taken during periods of arousal between hibernation bouts, no food is consumed; thus, little brown myotis may exit hibernation in the spring 25% lighter than when they entered in autumn.

Reproduction: Spermatogenesis begins in May and continues until late August when females enter estrus and copulation occurs. Copulations occur throughout autumn and into winter, as females begin to hibernate, indicating that this species may be seasonally polyestrous. Copulation with >1 male may occur; sperm from these inseminations are then stored in the female reproductive tract for up to 8 months. Stored sperm are held in close association with the uterine lining (Racey et al. 1987), which probably permits sperm to remain viable for an extended period of time. Ovulation occurs 1–3 days after permanent arousal from hibernation in the spring (Buchanan 1987), at which time conception occurs. After a gestation of 60 days, 1 young is produced. Postnatal growth is rapid, with attainment of adult body weight by day 16, and wing forearm growth by day 20 (Kunz and Anthony 1982).

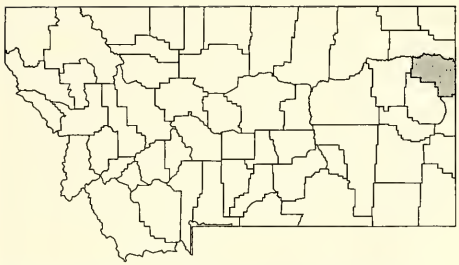
Status: Common.

Fenton, M. B., and R. M. R. Barclay. 1980. *Myotis lucifugus.* Mammalian Species 142:1–8.

Northern Myotis
Myotis septentrionalis

Scientific Name: The northern myotis was first described in 1897 by E. L. Trouessart from a type specimen collected in Halifax, Nova Scotia. Initially given the name *Vespertilio gryphus septentrionalis,* its status was changed to *Myotis keenii* by Miller and Allen in 1928. After research of van Zyll de Jong (1979), *septentrionalis* was accepted as a distinct species. The generic distinction, *Myotis,* is from the Greek combination myos, meaning "mouse," and otos, meaning "ear," thus "mouse-eared." The specific epithet *septentrionalis* is Latin for, "belonging to the north."

Description: The northern myotis is similar in size and general overall appearance to the other 7 *Myotis* species found in Montana. It is 1 of 5 species with relatively long ears, which are dark brown in color. When laid forward, ears extend beyond the muzzle about 2–4 mm. The border of the pterygium



Map 22. Distribution of the northern myotis, *Myotis septentrionalis*.

has a sparse distribution of stiff hairs and is almost black in coloration, as are the wings themselves. Dorsal body pelage is typically dark brown, with dark spots on the shoulders, and an overall glossy appearance; the ventral pelage is tan to buff in color. A small keel is present on the calcar. The northern myotis is often quite difficult to distinguish from other myotis, particularly the California myotis. It can be best distinguished by the glossy appearance of its pelage (that of the California myotis is non-glossy), and the presence of hairs (although sparse) on the pterygium. Small body size, and presence of a keel, can be used to distinguish this species from the Yuma myotis, little brown myotis, long-eared myotis, and fringed myotis.

Measurements: [mm(*n*); Smith 1993]: TL = ♂ 92.9(40)/♀ 94.3(10); Ta = ♂ 40.9(40)/♀ 43.0(10); HF = ♂ 10.4(40)/♀ 10.6(10); E = ♂ 17.8(40)/♀ 18.2(10); M [g(*n*)] = ♂ 6.6(40)/♀ 7.4(10). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The northern myotis occurs from the central and eastern United States to as far south as the Florida Panhandle. Only 1 specimen has been collected in Montana, this from the Culbertson Mine southwest of the town of Culbertson, in Richland County (Swenson and Shanks 1979). General distribution maps encompass the eastern most border of Montana, based upon records obtained from Wyoming, North Dakota, and Saskatchewan.

Ecology and Behavior: The basic ecology of the northern myotis is not well known, in part because it is less common than other myotis with which it is sympatric and because it appears to be more timid. Summer roost sites often include barns and cabins, as well as under the bark of trees. It forages under the canopy in more upland forested areas, away from the riparian zones preferred by *M. lucifugus*. Foraging activity begins just after sunset and tapers off throughout the night. A wide diversity of insect species are taken by this bat, with noticeable regional differences documented. In Indiana, the stomach of 1 individual contained 60% Hemiptera, 30% Hymenoptera, and 10% Homoptera, while another contained 70% Lepidoptera and 30% Diptera. In Missouri, a high percentage (by volume) of Lepidopterans, with significant occurrences of Trichopterans and Plecopterans, were reported.

Hibernation may begin in late summer when large numbers of individuals retreat to caves and mines, particularly those which present a cool, moist environment. The northern myotis is known to roost with other bat species, including the little brown myotis, eastern small-footed myotis, eastern pipistrelle, and big brown bat (Hitchcock et al. 1984). The single individual collected in Montana was an adult male obtained while hibernating in a mine in mid-January. Such a record now supports the year-round residency status of this species, although it is likely that migration from the state occurs in autumn.

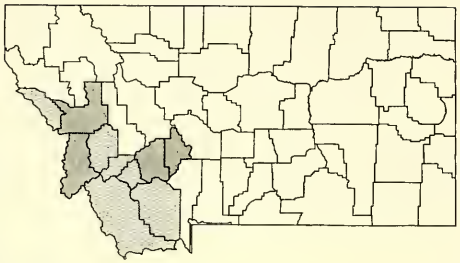
Reproduction: The reproductive biology of the northern myotis is poorly documented. It likely follows the pattern exhibited by other *Myotis*. See the discussion for reproduction in the little brown bat, *Myotis lucifugus*. In the Midwest, breeding occurs from late July into early October. Pregnant females have been observed between late May and late June; parturition has been documented from mid-May to mid-July.

Status: Rare and poorly understood.

Caceres, M. C., and R. M. R. Barclay. 2000. *Myotis septentrionalis*. Mammalian Species 634:1–4.

Fringed Myotis
Myotis thysanodes

Fringed myotis (*Myotis thysanodes*).



Map 23. Distribution of the fringed myotis, *Myotis thysanodes*.

Scientific Name: The fringed myotis was first described by Miller, from a type specimen obtained at Old Fort Tejon, Kern County, California by T. S. Palmer, in 1891. The generic designation, *Myotis*, is derived from the Greek generative combination, myos, which refers to "mouse," and otos, which refers to "ear;" "mouse-eared." The specific epithet, *thysanodes*, is from the Greek *thysanos*, meaning "fringed."

Description: The most distinguishing feature of this small *Myotis* is the well-developed fringe of hairs that lines the posterior edge of the pterygium, from which its vernacular name arises (Fig. 24). Color varies from light brown to yellowish-brown, although it may appear darker in more northern regions. Ears and wing membranes are black. This is a small-to-medium sized *Myotis*, with a wingspan of about 30 cm.

Measurements: [mm(*n*); O'Farrell and Studier 1980]: TL = ♂/♀ 43–59; Ta = ♂/♀ 34–45; HF = MT ♂ 10.0/♀ none; E = ♂/♀ 16–20; MT ♂ 16.0; M [g(*n*); Christy and West 1993] = ♂/♀ 5–7; MT ♂ 10.0. Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The fringed myotis is primarily found in the western United States extending from British Columbia southward throughout Mexico. Few records exist from Montana and these populations are on the northeastern-most limit of the range. The 1st record for Montana was in 1961 in Ravalli County (Hoffmann et al. 1969). Three additional specimens have been obtained from Jefferson and Missoula counties, and 2 have recently been collected in Lewis and Clark County (Dubois 1999). The fringed myotis may eventually be found in the southeastern region of the state, because individuals have been collected in Wyoming and South Dakota near the Montana border.

Ecology and Behavior: Records indicate that the fringed myotis occurs in a variety of habitats from low to mid-elevation grass, woodland, and desert regions, up to and including spruce-fir forests. In Montana, it has been collected in forested regions at lower elevations. Roost sites also span a variety of forms; populations have been found in caves (Lewis and Clark Caverns near Helena), mines, and buildings. Although the fringed myotis migrates in New Mexico and Arizona, no information exists for its residence status or migratory patterns in Montana. It is considered transitory in Montana.

As with other members of this genus, the fringed myotis possesses short, somewhat

rounded wings, most appropriate for slow, erratic flight. It likely feeds around the tree canopy; studies on food preferences indicated that beetles (order Coleoptera) and moths (Lepidoptera) are predominant components of the diet. Most foraging activity, at least in the southern United States, occurs 1–2 hours after sunset.

Reproduction: Little information exists on this species' reproductive biology, but the reproductive pattern of the fringed myotis is similar to other *Myotis* (see the discussion for reproduction in the little brown bat, *Myotis lucifugus*).

Because both adult females and juveniles have been collected in the summer, it is likely that breeding occurs in Montana.

Status: Rare.

O'Farrell, M. J., and E. H. Studier. 1980. *Myotis thysanodes.* Mammalian Species 137:1–5.

Long-legged Myotis
Myotis volans

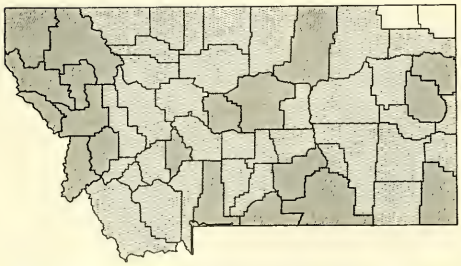
Scientific Name: The long-legged myotis was first identified as *Vespertilio volans* by Allen in 1866 from specimens collected from Cabo San Lucas, Baja California, Mexico. The current designation, *Myotis volans,* was first used by Goldman in 1914. The generic designation, *Myotis,* is derived from a Greek combination meaning "mouse-eared" [myos = "mouse," otos = "ear"]. The specific epithet, *volans,* is Latin for "flying."

Description: The vernacular name of the long-legged myotis alludes to the fact that its tibia (leg bone) is slightly longer than that of other *Myotis.* However, it can not be distinguished by the length of its legs, but rather by a combination of other characteristics such as a distinctly keeled calcar, very small rounded ears, and dense fur on the underside of the wing membrane that extends outward from the body to a greater degree than in other *Myotis.* Among Montana species, the long-legged myotis also is distinguished by a somewhat longer foot. Pelt color varies greatly among subspecies populations, ranging from yellowish-brown, through a darker reddish-brown, to even blackish-brown. Ears and wing membranes are characteristically black, and wings are short (27 cm) and slightly rounded. If careful observations can be made in hand, the long-legged myotis should not be confused with other *Myotis* in Montana. Presence of a distinctly keeled calcar will separate it from all but the California myotis and western small-footed myotis. Then the larger foot size will distinguish the long-legged myotis.

Measurements: [mm(*n*)]: TL = ♂ 95.3(3)/♀ 95.0(4); Ta = ♂ 42.3(3)/♀ 42.0(4); HF = ♂ 8.1(4)/♀ 8.4(4); E = ♂ 10.3(3)/♀ 12.3(3)M [g(*n*)] = ♂ 5.2(3)/♀ 6.9(4). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The long-legged myotis is common across the western one-half of the United States, with a range extending from northern British Columbia, across central Alberta, and then southward from the Dakotas to Texas and central Mexico. Specimens have been collected across Montana.

Ecology and Behavior: The long-legged myotis occurs most often in montane coniferous forest although specimens have been collected in riparian cottonwood woodlands along the Yellowstone River (Swenson and Shanks 1979). In Montana, many records have come from elevations >1,846 m (Hoffmann et al. 1969). Buildings, thick bark of trees, and caves provide



Map 24. Distribution of the long-legged myotis, *Myotis volans*.

summer roost sites (Worthington 1991); hibernacula are established in more protected caves and mine tunnels (Thomas and West 1991).

Foraging activity begins at sunset and is most apparent for the 1st several hours, although feeding has been observed throughout the night. The long-legged myotis is more tolerant of colder temperatures while foraging than species such as the little brown myotis, a fact that is supported by its occurrence at higher elevations. A wide variety of insects, notably moths (order Lepidoptera), lacewings (Neuroptera), leafhoppers (Homoptera), flies (Diptera), and beetles (Coleoptera) are taken. Although wings are intermediate in size and shape to those of most other *Myotis*, the long-legged myotis has a more direct, rapid pursuit pattern when chasing prey, often over longer distances.

Hibernating individuals were collected in December from the Culbertson Mine (near Culbertson, Richland County—Swenson and Shanks 1979), verifying year-round residency. However, many individuals may migrate out of Montana in autumn.

Reproduction: The long-legged myotis has a reproductive pattern typical of other *Myotis* (see the discussion for reproduction in the little brown bat, *Myotis lucifugus*). Due to the timing of fertilization, young may be born as early as May and as late as August. In Montana, pregnant females were collected on 9 and 17 July, and lactating individuals were obtained on 17 July (Jones et al. 1973; Lampe et al. 1974).

Status: Common and locally abundant.

Warner, R. M., and N. J. Czaplewski. 1984. *Myotis volans*. Mammalian Species 224:1–4.

Yuma Myotis
Myotis yumanensis

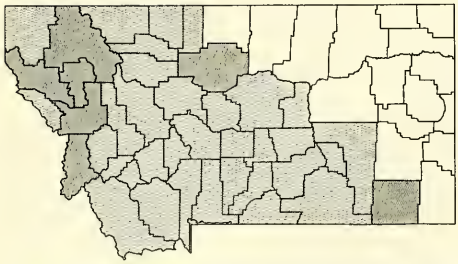
Yuma myotis (*Myotis yumanensis*).

Scientific Name: The Yuma myotis was first described as *Vespertilio yumanensis* by Allen (1864), from a type specimen from Old Fort Yuma, Imperial County, California, near where Yuma, Arizona, now exists. First use of the present nomenclature, *Myotis yumanensis*, was made by Miller (1897). The generic designation, *Myotis*, is derived from the Greek combination myos, which refers to "mouse-like," and otos, in reference to "ear," thus "mouse-eared." The specific epithet, *yumanensis*, acknowledges the site from which the type specimen was collected.

Description: The Yuma myotis is a small member of this genus and shows a wide range of color. The dorsal fur is non-glossy in appearance and ranges from black through reddish-brown to light brown, while the underfur is often a light brown to yellowish-white. Wing membranes and ears are brown. Calcar is unkeeled, and wing membranes have no distinguishing hair patterns. Wingspan falls within the range found for this genus, with an upper size of about 27 cm. The Yuma myotis can be distinguished from the California myotis, western small-footed myotis, and long-legged myotis by the absence of a keeled calcar. It is separated from the long-eared myotis and fringed myotis by the color of its wings and ears, and lack of a fringe of hair on its pterygium. Greatest difficulty is distinguishing the Yuma myotis from the little brown myotis. Here, overall body size is most useful (Yuma myotis weighs one-fourth to one-third less than the little brown myotis) and it has a non-glossy appearance of the dorsal fur.

Measurements: [mm(*n*)]: TL = ♂ 85.0(1)/♀ 78.8(8); Ta = ♂ 35.0(1)/♀ 35.8(8); HF = ♂ 10.0(1)/♀ 8.8(2); E = ♂ none/♀ 12.6(8); M [g(*n*)] = ♂ 5.3(1)/♀ 5.9(10). Dental formula: i 2/3, c 1/1, p 3/3, m 3/3, total 38.

Distribution: The Yuma myotis is found across the western United States and, like the fringed myotis, is on the northeastern limits of its range in Montana. Its range extends from central British Columbia, southward along the Pacific Coast to central



Map 25. Distribution of the Yuma myotis, *Myotis yumanensis*.

Mexico, with disjunct eastward extensions into Montana, Utah, Colorado, and southward into Texas. A majority of Montana's records come from western counties (Hoffmann et al. 1969). More recently, specimens were collected along the Missouri River in Choteau County and in Powder River County in the southeast—interesting because these records are east of the Continental Divide.

Ecology and Behavior: The Yuma myotis prefers to roost in buildings, bridges, caves, and mines during spring and summer. Although maternity colonies almost exclusively use human-made structures, hibernacula are always associated with caves and mines, which provide cooler environments. Yuma myotis begins to forage early in the evening just at dusk, although they may be observed prior to sunset (Whitaker et al. 1981). Unique among North American bats, the Yuma myotis feeds nearly exclusively over open water and, as such, establishes roost sites nearby such areas (Herd and Fenton 1983). It is a feeding generalist and forages opportunistically on aquatic insects (Brigham et al. 1992). The Yuma myotis has relatively shorter wings, with less wing surface area than the fringed myotis, a similarly-sized bat. Its wing structure produces a slower, less maneuverable pattern of flight and may explain why it forages most often over open water.

Reproduction: The reproductive pattern of the Yuma myotis is that typical of other *Myotis* (see the discussion for reproduction in the little brown bat, *Myotis lucifugus*). Females migrate from cave hibernacula to establish maternity colonies in buildings where the warmer conditions are conducive for developing young.

Status: Locally common in western Montana; may be found in close association with the little brown myotis.

ORDER LAGOMORPHA—PIKAS, HARES, AND RABBITS

The order Lagomorpha includes rabbits and hares (family Leporidae) and pikas (family Ochotonidae). Thirteen genera with 69 species are spread across most of the world; of these, 8 species occur in Montana. Rabbits and hares are easily recognized because of their posture, greatly enlarged hind feet and reduced fore feet that require them to rest on their haunches. When moving slowly, they are plantigrade (walking on the soles of the feet), but when running they become digitigrade (walking on the digits). The ordinal name, derived from the Greek, lagos, meaning "hare," and morphe, referring to "shape," reflects this unique body form.

Several unique skull and dental features are evident (Fig. 29). The skull in most species is highly fenestrated (perforated). A 2nd pair of upper incisors, lying directly posterior to the 1st, clearly identifies and separates this group from the rodents; a large diastema (space) is present between incisors and cheek teeth, incisors are evergrowing, and molariform teeth are hypsodont (possessing a high crown) and rootless.

All species are strictly herbivorous and are extremely efficient at digesting plants. They use a behavioral strategy of ingesting their own feces, termed coprophagy, allowing most foods eaten to pass through the digestive tract twice. This allows greater time for bacterial fermentation and thus digestion of food.

The difference between rabbits and hares is often confusing, in part perpetuated by the improper use of these vernacular terms. The term "hare" is most appropriately applied to members of the genus *Lepus*; species within the other 9 genera of the family Leporidae are correctly identified as "rabbits." This distinction is not simply 1 of semantics because anatomical and physiological features differ between these groups. Unfortunately, vernacular names are often applied to the wrong species (e.g., the black-tailed jackrabbit is actually a hare, *Lepus californicus*). The most important distinction is the condition of the young at birth. Newborn hares are born in a precocial condition; their eyes are open, and they are fully furred and able to run within a few minutes of birth. The female hare gives birth to her offspring in the open, with little attempt to provide a nest structure. Rabbits by comparison, are altricial at birth. They are born in a well-constructed nest in a helpless condition; naked, blind, and incapable of much coordinated movement. Additionally, hares are larger and less social than rabbits, and hares have a longer gestation period.

Fig. 29. Skull of a lagomorph (*Lepus*).

In Montana, we have 1 species of pika, 3 species of hares, and 4 species of rabbits.

Family Ochotonidae—Pikas

Pika
Ochotona princeps

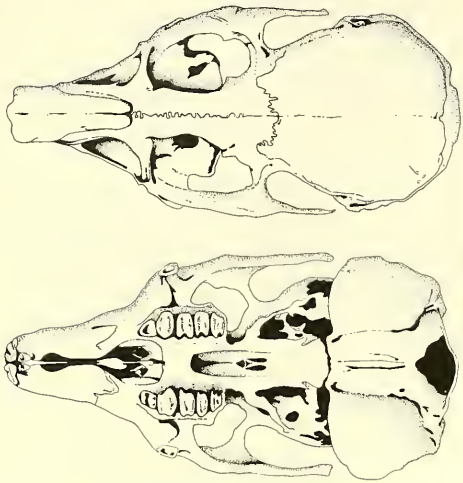


Fig. 30. Skull of the pika (*Ochotona*).

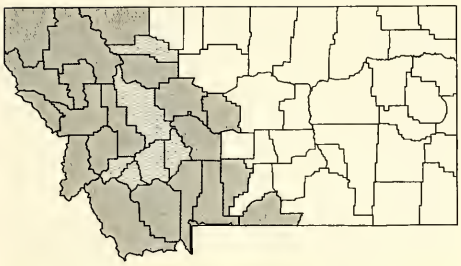
Pika (*Ochotona princeps*). See plate 2.

Scientific Name: The pika, also referred to as the "rock rabbit," or "cony," was first described by Richardson in 1828, as *Lepus* (*Lagomys*) *princeps*, based on specimens obtained by Captain Franklin's scientific expedition to the Rocky Mountains in the early 1800s. In 1897, Trouessart applied the current name to the species. The genus designation, *Ochotona,* is derived from the Mongolian name ochodona used to identify this animal, where several extant species exist. The specific epithet, princeps, is Latin for "chief." The Chipewyan Indian tribe referred to pikas as "little chief hare."

Description: The pika is the smallest lagomorph in Montana, with many unique physical characteristics that clearly separate it from other mammal species. It is a small animal, weighing about 150 g and measuring 20 cm in length. Rather than the elongated "rabbit" ears of other lagomorphs, it has small, rounded ears. The fore feet are nearly the same size as the hind feet, unlike the general conformation of rabbits and hares, and the small tail is not readily observable. Color is uniformly grayish to cinnamon-brown dorsally with a whitish-gray venter. The orbital region of the skull with marked backward bony projections is also unique (Fig. 30).

Measurements: [mm(*n*)]: TL = ♂ 180.9(10)/♀ 185.1(10); Ta = ♂ 0(10)/♀ 0(10); HF = ♂ 29.8(10)/♀ 30.3(10); E = ♂ 22.3(4)/♀ 22.8(8); M [g(*n*)] = ♂ 150.4(10)/♀ 147.1(10). Dental formula: i 2/1, c 0/0, p 3/2, m 2/3, total 26.

Distribution: The pika is the denizen of higher elevation rock slopes throughout the western United States, ranging from central British Columbia in the north southward as far as the mountains of California, Colorado, and New Mexico. In Montana, it is found in most central mountain ranges and all western ranges. Interestingly it is absent from the Big Snowy Mountains, near Lewistown, and the Bridger Mountains, north of Bozeman, where the



Map 26. Distribution of the pika, *Ochotona princeps.*

talus slopes may be too fine to be useable. No records are available from the smaller ranges of the eastern region, perhaps because they were once covered by glaciers.

Ecology and Behavior: The pika's continued association with higher elevation montane talus slopes may be a response to changing environmental conditions over the past several thousand years (Brown 1978). Suitable space between boulders is required for movement and construction of nest sites and precludes establishment of populations in scree fields of small diameter rocks (<0.2 m). Although nest sites occur within the recesses of such boulder fields, nearby meadows are as important, because these are required for forage.

Pikas are strict herbivores. They are not only selective in the plants chosen but their choice is based upon the nutritional quality of the plant species at a given time. In other words they are able to assess the changing quality of a particular plant as it develops and prefer to harvest the plant when it provides the highest caloric content. As an inhabitant of high-elevation, rocky slopes, the pika routinely experiences harsh winter climates. Because it does not hibernate and is strictly herbivorous, it stores the food it requires to sustain it over through the long winter. The accumulation and storage of this food occupies the pika throughout summer. Tall grasses and forbs are preferred storage items. These plants are deposited in "hay piles" constructed under rock ledges (Fig. 31). Each pika produces several of these hay piles, each of which may measure >1 m in diameter and >30 cm in depth. Where sympatric (occur together) with marmots, pikas also may use this species' feces as a supplemental energy source during winter (Gessaman and Goliszek 1989). Such feces contain higher useable energy than the most abundant vegetation normally collected by pikas, and marmot feces have been observed in pika's hay piles.

Pikas are solitary. Males and females establish independent home ranges and de-

Fig. 31. Typical appearance of a pika "hay" pile in mid-summer.

fend parts of these (their territories) at various times of the year. Initially, territories are based on habitat qualities—primarily the best rocky areas for nest sites and proximity to quality foods. As autumn approaches, pikas protect hay piles, so the defended part of the home range shrinks and is centered around these structures. Defense of territories may be aggressive, but the complex vocalization of pikas limit physical contact. Pikas are well known for the distinctive, sharp, high-pitched alarm calls that they use to warn neighbors of an approaching threat (be it a weasel or a human). When near a boulder field, this often is the 1st clue to hikers that pikas are present.

Pikas are active early morning and evening hours when ambient temperatures are cool. Easily heat stressed, pikas adjust to increasing temperatures by retreating underneath the boulder field. On overcast days, activity may be extended into the midmorning.

Reproduction: Breeding occurs in the spring as snowmelt begins. Pikas try to time parturition (birth) so that lactation, which is the most energetically costly time for females, begins when fresh vegetation appears. Gestation lasts 30 days, and the female exhibits a postpartum estrus, resulting in the production of 2 litters/year. Because breeding is tightly correlated with environmental conditions, which may be highly variable from 1 year to the next, a wide window of parturition dates can be found between populations. Litter sizes average 2.34–3.68 young and, although 2 litters are commonly produced, only 1, most often the 1st, is weaned.

Young grow rapidly and enter the main population within 4 weeks of age. A philopatric (parental recognition and support of offspring) social structure develops at this time; young attempt to live near their natal home range, and their parents recognize them and accept their presence. Aggressive conflicts between juveniles and parents are reduced by temporal separation of activity.

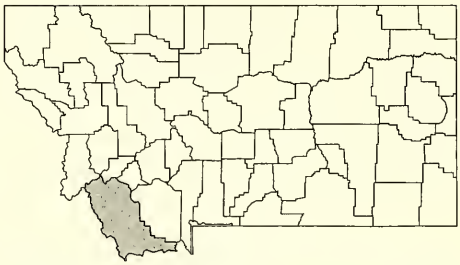
Status: Common in western and central Montana.

Smith, A. T., and M. L. Weston. 1990. *Ochotona princeps.* Mammalian Species 352:1–8.

Family Leporidae—Hares and Rabbits*

Pygmy Rabbit
Brachylagus idahoensis

Scientific Name: The pygmy rabbit was first described by C. Hart Merriam, Chief of the United States Biological Survey, as *Lepus idahoensis,* in 1891. The type locality from which specimens were obtained was the Pahsimeroi Valley in Custer County, Idaho. Lyon was the 1st to apply the current name, *Brachylagus idahoensis,* in 1904, in his revision of the hares and rabbits. The generic designation, *Brachylagus,* comes from the Greek, brachys, meaning "short," and lagos, meaning "hare;" a reference to this species' diminutive size. The specific epithet, *idahoensis,* denotes the state in which the type locality occurred.



Map 27. Distribution of the pygmy rabbit, *Brachylagus idahoensis.*

Description: As its name implies, the pygmy rabbit is small, the smallest leporid in North America. The hind feet and ears are shorter than in other Montana species, and the tail is comparatively smaller and distinctly brownish to grayish on both dorsal and ventral surfaces. In body color, the pygmy rabbit is buffy-gray, with patches of cinnamon on the nape of its neck and on the anterior surfaces of its legs. Several skull—dental characteristics also clearly distinguish this species (Foresman 2001). The pygmy rabbit could be confused easily with the 3 other rabbit species in Montana, genus *Sylvilagus.* A combined consideration of pelt color, body size, locality, and habitat association will separate these species. Although most similar in size, coloration, and habitat preference to the mountain cottontail, ranges of these 2 species do not overlap in Montana (however, in Idaho, they have actually been observed to occupy the same burrow system). One of the most reliable distinguishing characteristics is the color of the tail; in *Sylvilagus,* the ventral surface of the tail is always white.

Measurements: [mm(*n*); Davis 1939, MT collection of ID specimens]: TL = ♂ 262(4)/♀ 296(3), MT 240.0(1); Ta = ♂ 17.5(4)/♀ 20(3), MT 20.0(1); HF = ♂ 69.8(4)/♀ 72(3), MT 75.0(1); E = ♂ 49.3(4)/♀ 47(3), MT 55.0(1); M [g(*n*); MT specimens] = ♂ 465.0(1)/♀ 485.5(1). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: The pygmy rabbit is a Great Basin species whose distribution is centered in Idaho, Utah, Nevada, and Oregon. An isolated population exists in eastern Washington, a relic produced by the loss of sagebrush habitat over the past 3,000 years (Lyman 1991).

Ecology and Behavior: The pygmy rabbit prefers dense clumps of big sagebrush, or greasewood, within which they construct an extensive burrow system. They forage on grasses, particularly wheatgrass and bluegrass in summer, shifting almost exclusively to big sagebrush in winter. Foraging activity is confined to early morning and evening (a crepuscular pattern); other-

* For diagnostic skull characteristics of this family refer to Fig. 29 above.

wise, they rest at the entrances to their burrow. When moving, rather than bounding like other leporids, they adopt a "scampering gait," appropriate locomotion through a dense understory.

Pygmy rabbits, as with all other lagomorphs, are active year-round. At higher elevations, where snowcover occurs, subnivean burrow systems are developed to provide foraging access to foliage of big sagebrush.

Reproduction: The pygmy rabbit is a seasonal breeder. In males, testicular recrudescence occurs in January, with a peak in activity in March extending into June, when regression occurs. Females become receptive as early as February, producing a litter after a gestation period of 27–30 days. Up to 3 litters may be produced in a season, each containing 4–8 young; juveniles are not known to breed.

Status: Locally common.

Green, J. S., and J. T. Flinders. 1980. *Brachylagus idahoensis.* Mammalian Species 125:1–4.

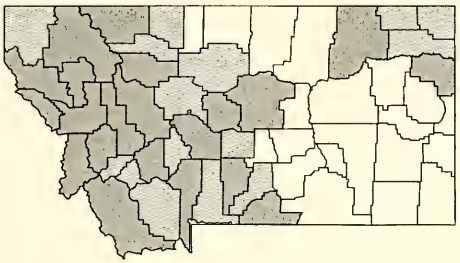
Snowshoe Hare
Lepus americanus

Snowshoe hare (*Lepus americanus*). See plate 3.

Scientific Name: The snowshoe hare was first described by Erxleben in 1777 from specimens collected at Hudson Bay, Ontario, Canada, the type locality (Hall 1981:315). The generic designation, *Lepus,* is the Latin term for "hare." The specific epithet, *americanus,* is the Latinized term for "America."

Description: The snowshoe hare is a large lagomorph, characterized by large ears and hind feet. The vernacular name, "snowshoe," refers to its enlarged, heavily-furred hind feet, the toes of which can be spread widely, providing a large surface area for support on soft snow. It has a predominantly brown pelage in summer, possibly flecked with black and distinct white edging on its ears. The tail is black above and white below, and hind feet retain a predominance of white hair. In winter, the snowshoe hare turns white, retaining black only on the tops of its ears. It may appear somewhat mottled because the underfur remains brown and can be seen through the long, white, winter guard hairs. Snowshoe hares can be readily distinguished from other lagomorphs in Montana by their large feet and ears (Fig. 32). The distinct white edging on the ears (summer pelage) is the most reliable characteristic separating this species from the 2 jackrabbits in Montana. Black coloration on its tail further distinguishes it from the white-tailed jackrabbit, *L. townsendii.* Measurement of ear length also is a useful characteristic (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 407.4(10)/♀ 407.3(7); Ta = ♂ 38.7(10)/♀ 38.7(10); HF = ♂ 132.4(10)/♀ 132.3(6); E = ♂ 76.5(10)/♀ 74.6(5); M [g(*n*)] = ♂ 1242.0(10)/♀ 1378.1(7). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.



Map 28. Distribution of the snowshoe hare, *Lepus americanus*.

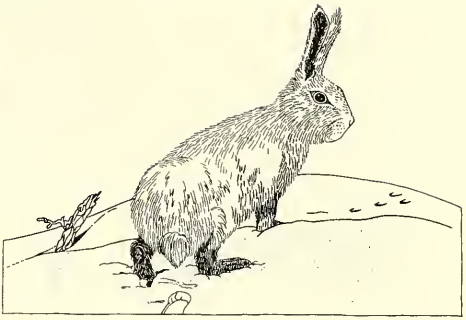


Fig. 32. Large, well-furred hind feet of the snowshoe hare provide a large surface area for support on soft snow.

Distribution: The snowshoe hare ranges widely across the northern tier of North America from Alaska to Newfoundland. In the western part of its range, it extends southward to New Mexico, and in the east it extends down the Appalachians to Tennessee.

Ecology and Behavior: Because the snowshoe hare was described >200 years ago, all aspects of its natural history have been, and continue to be, investigated. In part, interest in the snowshoe hare stems from its prominence throughout the Canadian provinces as the major prey species for lynx. Indigenous to the boreal forests of North America (Dolbeer and Clark 1975), this species prefers habitat that provides a dense understory of coniferous vegetation for protective cover and winter browse (Buehler and Keith 1982). Deciduous cover, such as alder and willow, may also be used extensively. The snowshoe hare uses a variety of habitats, as long as the quality of cover provided is adequate (Pietz and Tester 1983). In Montana, preference is given to dense stands of pole-size Douglas fir, particularly those with heavy-structured ground litter, such as tree limbs and dead saplings (Adams 1959).

Spring and summer forage consists of a variety of herbaceous species: grasses, sedges, ferns, and leaves of deciduous trees. In autumn and winter, a shift is made to twigs and buds of deciduous, and coniferous species, conifer needles, mosses, and lichens (Smith et al. 1988). Woody browse <3 mm in diameter provides optimal nutritional quality; twigs larger in diameter are of lesser quality and are only eaten when hare numbers are excessive and quality browse becomes limiting (Pease et al. 1979).

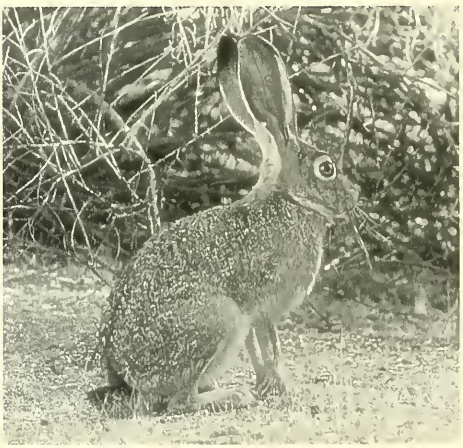
The snowshoe hare is well known for the cyclic nature of its population. Cyclic fluctuations, with an 8–11 year period, have been recorded for >200 years (Keith 1963). During a 15-year study in Alberta (Keith and Windberg 1978), a 23-fold change in numbers of hares was noted between lowest and highest spring densities, with upper levels of 23 hares/ha. The driving force behind these cycles is not fully understood, but winter food shortage may precipitate the initial population decline. With lower numbers of snowshoe hares, the predator–prey ratio is skewed in favor of predators further depressing hare populations. Poor quantity and quality of forage in turn acts to depress reproductive output. At the population low of hares, predator numbers are reduced due to unavailability of food (causing death or dispersal), while at the same time vegetation is recovering due to lessened grazing pressure. At this point, conditions improve for renewed growth in the hare population; the greater abundance of food enhances reproductive output, growth, and survival of offspring. Clearly, predator–prey relationships (lynx–snowshoe hare, hare–vegetation) are the fulcrum on which cycles turn; however, many environmental and physiological factors intertwine to drive these changes.

Reproduction: Studies conducted by Adams (1959) in the northwestern region of Montana (Bull Island in Flathead Lake), provided detailed information on reproductive biology of the snowshoe hare in Montana. Male sexual development begins in late February–early March. Successful copulations apparently can occur within 2 weeks because pregnancies have been observed in mid-March. The breeding season ends in early to mid-July, with the last litters born in early August. With a gestation length of 35 days and post-partum estrus, up to 4 litters may be produced each season. Adams (1959) recorded an average of 2.9 litters/season, with 2.6–3.0 young/litter. Young are weaned at about 45 days of age; those born in early summer reach adult weight in autumn to early winter, but they do not breed until the following spring.

The snowshoe hare apparently does not build a nest but relies on brush cover and precocial (rapid) development of the young for protection.

Status: Common although population levels fluctuate widely.

Black-tailed Jackrabbit
Lepus californicus



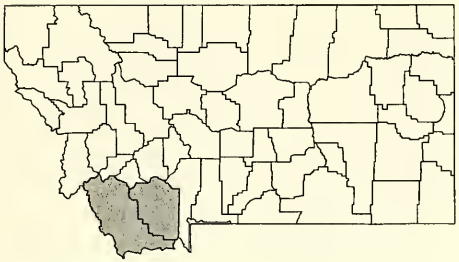
Black-tailed jackrabbit (*Lepus californicus*). See plate 3.

Scientific Name: The black-tailed jackrabbit was first described by Gray in 1837 from a type specimen collected in Monterey County, California. The generic designation, *Lepus,* is Latin for "hare." The specific epithet, *californicus* is the Latinized word for California, where the type specimen was obtained.

Description: The black-tailed jackrabbit, as the vernacular name implies, has distinctly black colored hairs on the dorsal surface of its tail; the ventral surface is white. Body color varies from gray to blackish. Unlike the other 2 species of *Lepus* in Montana, the black-tailed jackrabbit does not change color in winter. This is a large-bodied lagomorph with large ears and hind legs. Body conformation (extremely large ears and feet) readily separates the black-tailed jackrabbit from the pika, pygmy rabbit, and cottontail rabbits of the state. Ear length and color can distinguish it from the snowshoe hare (*L. americanus*); length of the hind foot and distinct coloration of the tail separates it from the white-tailed jackrabbit, *L. townsendii* (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 550(2)/♀ 587.0(4); Ta = ♂ 84.0(2)/♀ 84.8(4); HF = ♂ 125.5(2)/♀ 134.9(4); E = ♂ 122.0(2)/♀ 135.3(3); M [g(*n*)] = ♂ 2,032.0(2)/♀ 2,602.3(4). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: The black-tailed jackrabbit has an extensive range covering a majority of the western two-thirds of the United States extending from California to Missouri and north–south from Washington to central Mexico. It is confined to the



Map 29. Distribution of the black-tailed jackrabbit, *Lepus californicus.*

southwestern corner of Montana where it may be found in sympatry with the white-tailed jackrabbit.

Ecology and Behavior: In western and southern regions, the black-tailed jackrabbit prefers sagebrush desert and semi-desert habitats; to the east, it is found in more open grasslands and cultivated fields. As with other lagomorphs, this jackrabbit is strictly herbivorous feeding on a variety of herbaceous plants in the spring and summer, switching to woodier materials in autumn and winter. Foraging occurs in the early evening. During the day, animals rest in "forms," shallow depressions carved out of the ground or surrounding vegetation. Coprophagy, the reingestion of feces, occurs. Soft-bodied green feces, produced initially, contain high quantities of B vitamins thought to result from bacterial activity in the caecum. These feces are reingested as they are excreted, whereupon the vitamin component can be extracted. Subsequent feces are dry and dark brown in color.

Whereas cottontail rabbits have a scampering gait and run low to the ground through brush, jackrabbits are easily recognized by their bounding gait. Individuals cover distances of 1.5–3 m at a jump when moving undisturbed; when frightened they may bound 5–10 m (Schwartz and Schwartz 1959). An interesting behavioral pattern also is incorporated into these escape movements. At every 4th to 5th jump, the animal springs higher into the air (sometimes as high as 1.5 m) in an apparent attempt to get a better view (Fig. 33). Short bursts of

Fig. 33. Jumping behavior of the jackrabbit when excited.

speed, up to 35 mph, are not uncommon when a black-tailed jackrabbit is excited, making capture difficult for predators such as coyotes, bobcats, and foxes.

The black-tailed jackrabbit is most often solitary. Although large aggregations may form at a particularly good feeding site, no regular social organization occurs. Aggressive acts are few but, when forced, a jackrabbit can defend itself with its large hind feet and may "box" with its forefeet.

Reproduction: No reproductive information is available for the black-tailed jackrabbit in Montana. A general overview is provided here from research on populations in California. Testicular development and spermatogenesis begins in November and reaches its peak in January, continuing until mid-to-late July. Sexually mature males, however, may be found any month of the year. Females may also breed in any month, although most breed between January and July. Gestation is from 41–47 days ($\bar{x}$ = 43 days) and because females exhibit a post-partum estrus, most are pregnant

and lactating concurrently. With an average litter size of 2.3 and an average number of pregnancies of 4.27/season, a female can produce 9.8 young/year. Young are precocial at birth, growing rapidly to reach adult body size within 7–8 months.

Reproductive seasons in California are influenced by the amount of green vegetation available, which is controlled by the amount of rainfall in a given season. Breeding activity of black-tailed jackrabbits in Montana occurs within a shorter period than in California.

Cyclic population fluctuations of the black-tailed jackrabbit are common in the Great Basin. Such fluctuations are localized and may reflect overcrowding and food shortage (Woodbury 1955).

Status: Locally common with marked annual population fluctuations.

Best, T. L. 1996. *Lepus californicus.* Mammalian Species 530:1–10.

White-tailed Jackrabbit
Lepus townsendii

White-tailed jackrabbit (*Lepus townsendii*).

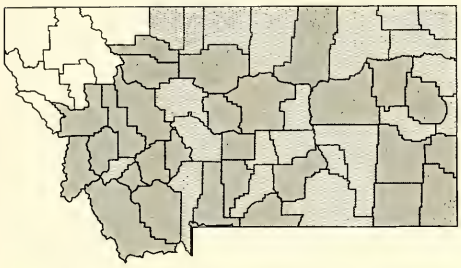
Scientific Name: Dr. John Bachman, a close friend of John James Audubon, was the first to describe this species. It was originally identified as *Lepus campestris* from specimens collected in Saskatchewan, Canada, in 1837 and was reassigned to *L. townsendii* by Hollister in 1915, based on specimens previously identified from Walla Walla County, Washington, in 1839. The generic designation, *Lepus,* comes from the Latin term for "hare." The specific epithet, *townsendii,* is in honor of J. K. Townsend who is credited with collecting the type specimen.

Description: As the vernacular name implies, the white-tailed jackrabbit has a distinct white tail on both dorsal and ventral surfaces. Summer body color is yellowish- to grayish-brown on the dorsal region blending into a lighter gray to white on the ventral surface. This species turns completely white in winter, except the tips of its ears, which remain black. Measurement of the hind foot and ears separates this jackrabbit from other lagomorphs in Montana, with the exception of the black-tailed jackrabbit (Foresman 2001). Here, the distinction is readily made based upon tail color; top of the tail of the black-tailed jackrabbit is distinctly black.

Measurements: [mm(*n*)]: TL = ♂ 613.9(10)/♀ 550.5(4); Ta = ♂ 101.5(10)/♀ 90.4(4); HF = ♂ 143.0(10)/♀ 129.6(4); E = ♂ 116.1(10)/♀ 130.3(4); M [g(*n*)] = ♂ 2772.6(10)/♀ 2818.1(4). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: The white-tailed jackrabbit is found throughout the northwestern United States, extending from central Saskatchewan to New Mexico.

Ecology and Behavior: The white-tailed jackrabbit inhabits a wide range of vegetative communities throughout Montana, although it is most commonly associated with open grassland plains, particularly east of the Continental Divide. In the western part of Montana it ranges from lower ele-



Map 30. Distribution of the white-tailed jackrabbit, *Lepus townsendii.*

vation valleys up to, and including, alpine tundra. As a strict herbivore, it relies on fresh grasses and forbs when available, turning to more woody shrubs in winter. Commercial crops, such as alfalfa, are highly prized.

Similar to most other leporids, the white-tailed jackrabbit is predominantly asocial; however, pockets of food, particularly during winter, may cause aggregations to form. Foraging activity is strictly nocturnal; daytime is spent resting, although little attempt is made to hide.

Winter and summer molts occur yearly allowing this jackrabbit to change its coat color with the season. This change protects it from predators. Such molts also provide a thicker winter pelt, that reduces overall thermal conductance and subsequent energy expenditure during the coldest months (Rogowitz 1990).

Reproduction: Although the breeding season in Montana is not well understood, it probably is similar to that of populations in North Dakota and Wyoming (Rogowitz 1992). In these adjacent states, breeding begins in late February, following testicular recrudescence, and extends into July, at which time the testes regress. Gestation lengths of between 4–6 weeks extend parturition into late summer. Litter sizes average 4–5. Females have a post-partum estrus; thus, breeding can occur soon after birth. This reproductive strategy allows females to produce up to 4 litters/year, with an average annual output of about 15 offspring (some prenatal mortality is observed). Young likely do not breed until they are at least 7 months of age.

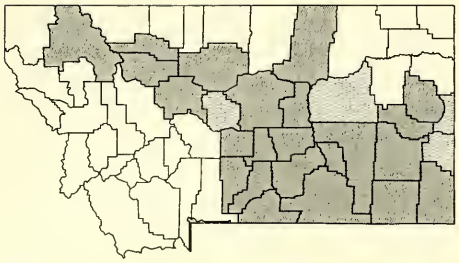
Status: Common.

Lim, B. K. 1987. *Lepus townsendii.* Mammalian Species 288:1–6.

Desert Cottontail
Sylvilagus audubonii

Desert cottontail (*Sylvilagus audubonii*).

Scientific Name: The desert cottontail was first described by Spencer Fullerton Baird, the founder of the United States National Museum, in 1858, from specimens collected in San Francisco, California, the type locality. Baird originally designated this species as member of the genus *Lepus.* Nelson correctly placed it into the genus *Sylvilagus* in 1907, and was thus the 1st to use the current name. The generic designation, *Sylvilagus,* is a combination of Latin and Greek: sylva, the Latin term for "a woods or forest," and lagos, which is Greek for "hare." The specific epithet, *audubonii,* is in honor of John James Audubon, the noted naturalist and artist.



Map 31. Distribution of the desert cottontail, *Sylvilagus audubonii.*

Fig. 34. Daytime rest sites of the desert cottontail in a hollowed out "form."

Description: Although coat color varies among species of *Sylvilagus* in Montana, the desert cottontail can often be distinguished from others by a slightly orangish patch of fur on its chest. Dorsal fur is pale and gray in color, with a slight tan appearance. The most distinguishing characteristic is the sparse distribution of hair on the inner surface of its ears; ears are also longer (generally >62 mm) than other cottontails. In general body form, the desert cottontail should not be confused with members of either the genus *Lepus* or *Ochotona.* Measurement of the hind foot easily identifies this species as a cottontail and also separates it from the pygmy rabbit (Foresman 2001). Among *Sylvilagus,* the desert cottontail can be distinguished by the reduction in hair within the ears, slightly longer ears, and overall lighter body color, and the orangish chest patch.

Measurements: [mm(*n*)]: TL = ♂ 433.3(6)/♀ 387.6(8); Ta = ♂ 46.6(7)/♀ 42.9(8); HF = ♂ 94.4(9)/♀ 93.8(8); E = ♂ 75.1(9)/♀ 65.7(6); M [g(*n*)] = ♂ 1038.6(8)/♀ 555(1; immature). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: As its vernacular name suggests, the desert cottontail primarily inhabits arid regions of the western United States from Montana to central Mexico. Populations exist from the Pacific coastal regions of California to the Dakotas and Texas. It is absent from the northwestern part of the country and from the sagebrush desert regions of Beaverhead County where the mountain cottontail, *S. nuttallii,* is found.

Ecology and Behavior: The desert cottontail inhabits arid, open areas, typically in upland grasslands and upland breaks. Such grasslands are dominated by sage and buffaloberry, with the occasional stand of ponderosa pine. Upland breaks are "true" badlands consisting of steep vertical faces of bentonite clay, and bedrock, with little vegetation. In the absence of the eastern cottontail, the desert cottontail will use more mesic sites such as river bottoms (Brown 1978).

Foraging occurs in early morning and early evening, predominantly on grasses, sedges, and some woodier materials, such as willow. At these times, foraging occurs close to, or within, brushy areas adjacent to open grasslands; at nighttime individuals can be found some distance from cover. During the day, individuals rest in "forms," shallow depressions that have been cleared near their burrow entrances (Fig. 34). Although they do not exhibit a strong social structure, they will feed with other members of the same species, and among species of jackrabbits without conflict.

Reproduction: Timing of the breeding season of desert cottontails in Montana is unknown. Reports from California and Arizona indicate that it may extend from

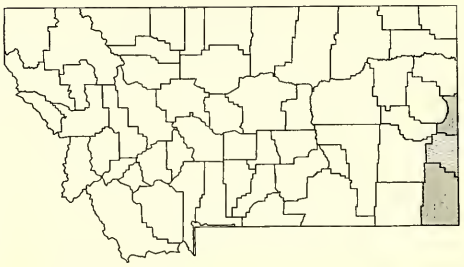
December–January to June, and even into August. Gestation is 28 days, and litter sizes are reported to be small, averaging 2.7–3.6 young. Several litters are probably produced each year.

Status: Common in arid regions.

Chapman, J. A., and G. R. Willner. 1978. *Sylvilagus audubonii.* Mammalian Species 106:1–4.

Eastern Cottontail
Sylvilagus floridanus

Scientific Name: The eastern cottontail was first described by Dr. John Bachman, in 1837, although his account failed to address the type locality from which specimens were obtained. Bachman identified this species as a member of the genus *Lepus,* specifically as *Lepus sylvaticus,* a name which means "hare which grows among trees." Allen was 1st to apply the current name to this species in 1890, in his description of a type specimen from Brevard County, Florida. The generic designation, *Sylvilagus,* is derived from a combination of the Latin term silva, which means "forest," and the Greek term lagos, which means "hare," thus "forest hare." The specific epithet, *floridanus,* is a Latinized term identifying the state from which the type specimens were obtained.



Map 32. Distribution of the eastern cottontail, *Sylvilagus floridanus.*

Description: The eastern cottontail is the largest rabbit in Montana. It has a rather dense long coat that varies from brown to gray, intermixed with black hairs, giving this species a distinctly grizzled appearance. Ventral color for both body and tail is white. Because of the eastern cottontail's restricted occurrence in Montana, it should not be confused with any other lagomorph in the field. The relatively larger body size and distinctive black dorsal pelage, should adequately distinguish it from other lagomorphs in Montana.

Measurements: [mm(*n*); range of measurements from unidentified sex, Hall 1981]: TL = ♂/♀ 375–463, MT ♂ 420.0(1); Ta = ♂/♀ 39–65, MT 43.0(1); HF = ♂/♀ 87–104, MT ♂ 105.0(1); E = ♂/♀ 49–68, MT ♂ 56.0(1); M [g(*n*)] = ♂/♀ none. Dental formula: 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: The vernacular name reflects widespread distribution of this cottontail throughout the eastern United States. It extends from Canada to southern Mexico and southwest as far as Arizona, having the most extensive range of any species of *Sylvilagus.* Montana is on the northwestern extreme of its range. Here, it is only found in the eastern one-third of Carter County (Lampe et al. 1974) and in Wibaux County in limited numbers.

Ecology and Behavior: With such a wide geographic distribution, the eastern cottontail occurs in a variety of habitats. Populations inhabit regions as diverse as deserts and swamps, hardwood forests, and rainforests. In Montana, it has only been found along riparian habitats, notably the Little Missouri River and Boxelder Creek, Carter County (Lampe et al. 1974). In nearby southwestern North Dakota, significant

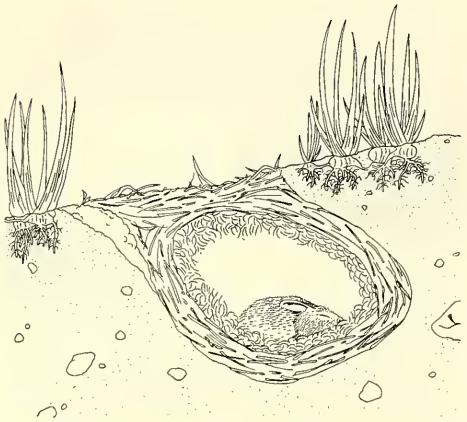


Fig. 35. Typical nest construction of the eastern cottontail.

use of terraces (consisting of rose, gooseberry, and hawthorn shrub cover) and hardwood draws (dominated by rose, hawthorn, and buckbrush shrub cover with box elder and green ash) occurs (Bergeron and Seabloom 1981). Where the eastern cottontail is sympatric with the mountain cottontail, which has similar habitat affinities, it displaces the latter form (Lampe et al. 1974). The eastern cottontail has also displaced the mountain cottontail in southeastern Montana, as it is now only found in the western part of Carter County.

The eastern cottontail constructs a nest in the ground from an angled hole, about 18 cm long and 10 cm deep, which it lines with grass, leaves, and its own fur (Fig. 35). When inactive above ground, it lies in "forms," depressions constructed from grass and bushes with a single opening, that provide hiding cover. During winter, underground burrows of other species may be used (Schwartz and Schwartz 1959). Outside of the breeding season, individuals are not territorial and home ranges overlap extensively.

Forage consists of a variety of herbaceous species consumed primarily during spring and summer; woody species may be eaten during winter when green vegetation is unavailable. As with other lagomorphs, coprophagy (ingestion of feces) is common. Foraging activity is bimodal, occurring a few hours after sunrise and again within 1–2 hours after sunset.

A social hierarchy develops, with dominant males and females establishing themselves through agonistic behavior. Aggressive activities occur between dominant and subordinate individuals, but actual physical confrontations are few. Dominant males are the most successful breeders.

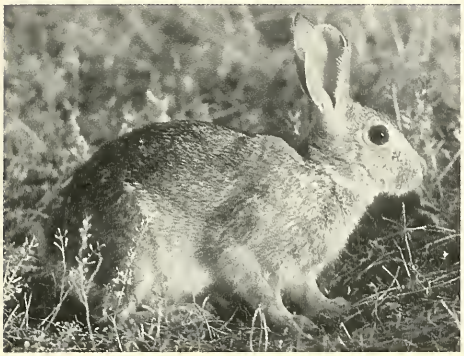
Two molts occur each year, the 1st beginning in early autumn leading to a thick winter pelage, and the 2nd, the spring molt, providing a thinner, cooler pelage for summer.

Reproduction: The breeding season in Montana is probably similar to that of eastern cottontails transplanted to Oregon. There, breeding begins in late January and continues until early September. Photoperiod, temperature, and availability of green vegetation likely affect timing of breeding. A mean gestation of 28–29 days and postpartum estrus allow 5–7 litters to be produced/season. Litter sizes range from 3.1–5.6 young, with larger numbers produced in more northern latitudes. Young are altricial at birth; eyes open on day 5 or 6 and movement from the nest is possible by day 12. Juveniles (young-of-the-year) can breed. It has been estimated that a single female could produce 24–35 young in a season.

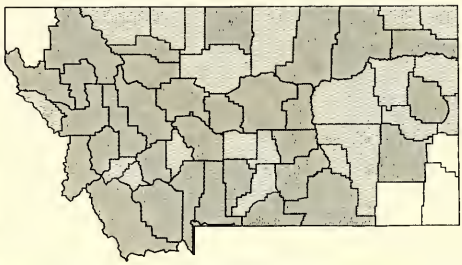
Status: Uncommon.

Chapman, J. A., J. G. Hockman, and M. M. Ojeda C. 1980. *Sylvilagus floridanus.* Mammalian Species 136: 1–8.

Mountain Cottontail
Sylvilagus nuttallii



Mountain cottontail (*Sylvilagus nuttallii*).
See plate 3.



Map 33. Distribution of the mountain cottontail, *Sylvilagus nuttallii*.

Scientific Name: The mountain cottontail was first described by Dr. John Bachman in 1837 from specimens obtained by Thomas Nuttall in 1834 at the mouth of the Malhuer River, Malhuer County, eastern Oregon. Bachman at the time named this species as *Lepus nuttallii*, a scientific distinction that was subsequently changed to the currently accepted form by Lyon in 1904. The generic designation, *Sylvilagus*, is from the Latin silva, meaning "forest," and the Greek *lagos*, which means "hare," thus "forest hare." The specific epithet, *nuttallii*, is the Latinized name honoring the 1st collector. Thomas Nuttall was best known as an ornithologist, a botanist, and curator of Harvard's botanical gardens.

Description: The mountain cottontail is a large rabbit, most similar in size and appearance to the eastern cottontail. The short ears have inner surfaces that are well-haired. Its dorsal pelage is brown to gray, with little if any black mixed in; the belly is white and the tail is bicolored. The mountain cottontail can be distinguished from other Montana lagomorphs by presence of fur on its inner ear surfaces (excludes the desert cottontail), and absence of significant black dorsal fur (excludes the eastern cottontail).

Measurements: [mm(*n*)]: TL = ♂ 351.5(9)/♀ 369.5(9); Ta = ♂ 35.9(9)/♀ 33.4(6); HF = ♂ 86.0(9)/♀ 90.0(9); E = ♂ 65.3(8)/♀ 58.6(8); M [g(*n*)] = ♂ 829.6(9)/♀ 855.9(10). Dental formula: i 2/1, c 0/0, p 3/2, m 3/3, total 28.

Distribution: The mountain cottontail ranges over the intermountain west where it extends from Canada to Arizona and New Mexico and from North Dakota to Oregon, Washington, and California. It has been displaced in the southeastern corner of Montana (Carter County) by the westward expansion of the eastern cottontail.

Ecology and Behavior: The mountain cottontail occurs in a variety of habitats from sagebrush slopes and willow patches to cultivated fields. It is associated closely with rocky outcroppings found in steep canyons and ravines, but it also has been found in dense, brushy riparian areas in central and eastern Montana (Hoffmann et al. 1969). When found in rock outcrops, it establishes burrows in crevices. Shallow burrows and forms are constructed in more open habitat under sagebrush or other shrubs.

Foraging behavior is similar to that of other lagomorphs. Most time is spent feeding in dense cover. Open grassy areas are used only if cover is near. Mountain cottontails are crepuscular; most activity occurs within a few hours after sunrise and just before sunset. In central Oregon, mountain cottontails climb into juniper trees by scampering up those which are acutely leaning. Once in the tree, they would move out onto larger limbs and feed on the foliage, and lick moisture that accumulated on the boughs. This is the 1st report of climbing activity in a lagomorph (Verts et al. 1984).

The mountain cottontail is not social; the only interactions occur during the breeding season.

Reproduction: The breeding season lasts from February or April in California, to July in Oregon. Four to 6 young are produced after a gestation of 28–30 days. Four to 5 litters are produced/season. Young are born into a shallow nest lined with grass and the mother's fur. No reproductive information is available for Montana.

Status: Common.

Chapman, J. A. 1975. *Sylvilagus nuttallii.* Mammalian Species 56:1–3.

ORDER RODENTIA

Rodentia is the largest taxonomic order of mammals in the world, encompassing 29 families, 380 genera, and close to 1,700 species. With a nearly worldwide distribution, rodents fill almost every ecological niche. Although most species are terrestrial, many such as pocket gophers of North America and mole rats of Africa and Asia are highly adapted for fossorial living. Others, such as tree squirrels, are arboreal (live in trees). Still others, the beaver and muskrat being excellent examples, adopted a semiaquatic life style. Rodents include some of the smallest mammals in the world (the pygmy mouse, *Baiomys,* of the southwestern United States weighs 5 g), to some very large species (capybara, *Hydrochaeris hydrochaeris,* of Panama can weigh as much as 79 kg).

Although this order is highly diverse, members share many characteristics. Rodents lack distinctive canine teeth, and their 4 incisorform teeth (2 above and 2 below) are "ever-growing," continually progressing outward from the base of the jaw in an arc. Constant grinding of upper and lower teeth is required to maintain a beveled, functional "chisel" for cutting vegetation. The absence of canines and anterior premolars causes a distinctive gap (termed a "diastema"; refer to Fig. 36) between incisors and molariform teeth (such a gap is also present in ungulates). The hard enamel surface of the molariform teeth is highly convoluted and intertwined with the softer dentine layer thrown into patterns. This tooth structure greatly increases surface area of the enamel layer, providing a longer lasting tooth, necessary because rodents, as herbivores, always eat abrasive foods. Many species also possess molariform teeth that are ever-growing, similar to the incisorform teeth, which also offsets tooth wear.

Of the 218 rodent species in North America north of Mexico, 45 exist in Montana. Members of this order thus make up a high percentage (42%) of the species within the state. We are fortunate to have representatives of 8 families and 27 genera, which exhibit the wide array of specializations found in this group and provide us with a diverse rodent fauna to enjoy.

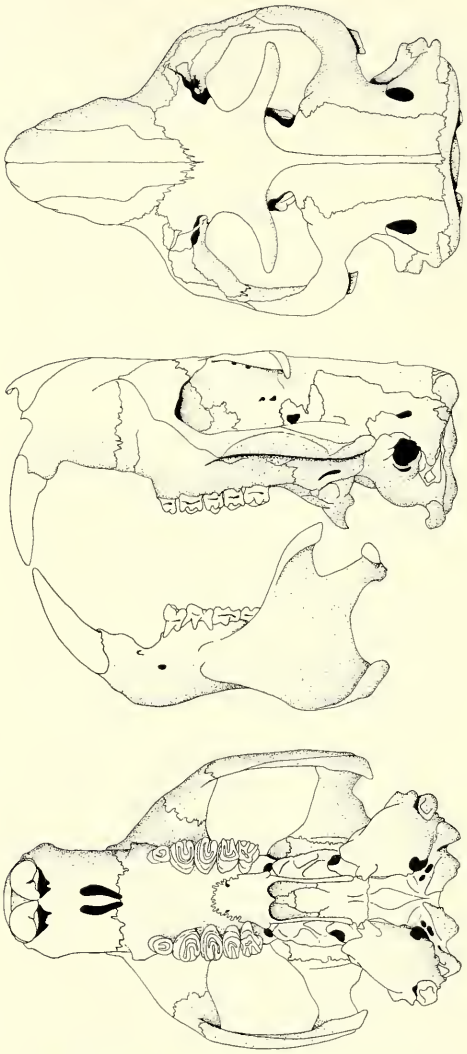


Fig. 36. Skull of a typical rodent (*Marmota*).

Family Castoridae—Beaver*

Beaver
Castor canadensis

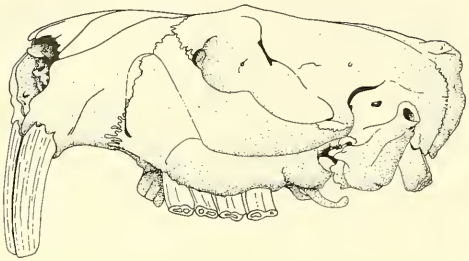


Fig. 37. Skull of the beaver (*Castor*).

Beaver (*Castor canadensis*). See plate 4.

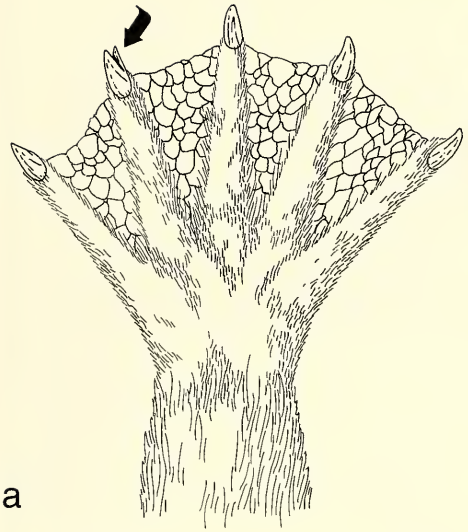
Scientific Name: Beavers were first described by Kuhl, in 1820, from specimens taken at Hudson Bay, Canada, the type locality. Kuhl applied the taxonomic distinction *Castor canadensis,* which is still accepted today. The generic designation, *Castor,* is Greek for "beaver;" the specific epithet, *canadensis,* denotes the country from which the species was first described.

Description: The largest rodent in the United States, beavers measure nearly 1.25 m in length and can weigh >39 kg, although 12–25 kg is more common. The beaver has many distinctive physical features, among which are the very small opening in the skull immediately in front of the eye socket (Fig. 37 and compare to Fig. 42) and the highly webbed toes of the enlarged hind feet with a split claw on the 2nd digit (Fig. 38a). These "grooming claws" allow the animal to comb oils from abdominal glands into their fur to keep it supple and water repellent. The large, dorsoventrally-flattened tail, which is scaled and nearly naked (Fig. 38b), serves as a fat storage site during winter and is important in thermoregulation during summer. Fore feet are small, and the fur is extremely dense, with fine gray underfur and coarse guard hairs. Air trapped among hairs functions like a thermopane window, providing insulation in cold water. Additional specializations for their aquatic environment include valvular ears and nostrils that keep out water, lips that close behind incisors allowing the animal to gnaw branches underwater, and transparent membranes that cover the eyes so that the animal can see clearly underwater. Pelt color ranges from reddish-brown to nearly black, although lighter forms occur. Beavers should not be confused with any other mammal in Montana. The only other semiaquatic species of size, found in sympatry with the beaver, is the muskrat (*Ondatra zibethicus*) which is much smaller, has only partial webbing between the toes of the hind feet, and has a narrow laterally-compressed tail.

Measurements: [mm(*n*)]: TL = ♂ 1035.0(1)/♀ 1024.4(7); Ta = ♂ 300.0(1)/♀ 260.6(7); HF = ♂ 177(1)/♀ 161.7(2); E = ♂ none/♀ 34.8(2); M [kg(*n*)] = ♂ none/♀ 17.0(7). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The beaver is one of the most widely distributed species in North

* For representative skull characteristics of this taxonomic family refer to Fig. 37.



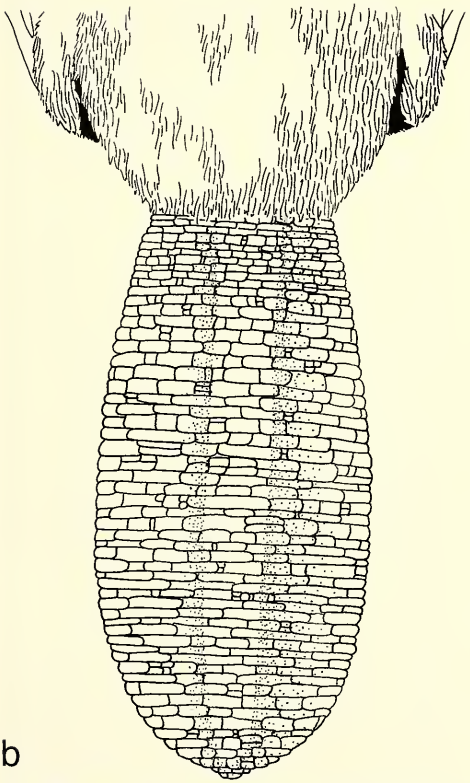
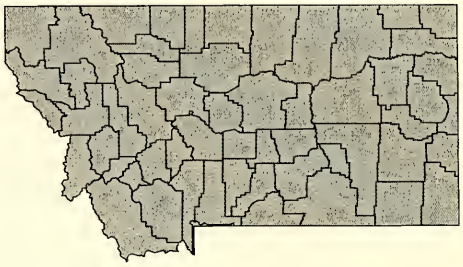


Fig. 38. Appearance of a) webbed hind foot with grooming claw on the 2nd digit (arrow) and b) scaly tail of the beaver.



Map 34. Distribution of the beaver, *Castor canadensis.*

America. With the exception of the Peninsula of Florida, deserts of the Southwest, and the high arctic tundra, it may occur wherever riparian habitat exists.

Ecology and Behavior: The beaver is a denizen of streams, lakes, and ponds. It is famous for the elaborate nests ("lodges") that it constructs out of trees and mud (Fig. 39). These structures, sometimes 6–9 m across and 2 m high, are constructed in the middle of a pond, or against the bank. The inner chamber, which lies just above waterline, is accessed by 1–2 underwater tunnels. A ventilation hole opens above water. The chamber is lined with grass and bark, increasing its insulating capacity, and providing a secure nest for the young. In larger rivers, tunnels may be excavated directly into a mud bank for many meters, at the end of which a den is constructed; the entrance to this burrow is usually below waterline. The lodge provides protection from predators and the elements throughout the year. Although ambient temperatures may fluctuate greatly in winter, beavers in a lodge experience only a few degrees variation in surrounding temperature (Dyck and MacArthur 1993). The insulating capacity of the lodge walls and the heat generated by groups of up to 8 individuals huddling together maintain lodge temperatures slightly above freezing, even although ambient temperatures may plunge far below zero.

Beavers are also well-known for their ability and eagerness to dam up streams, creating "beaver ponds." The sound of run-

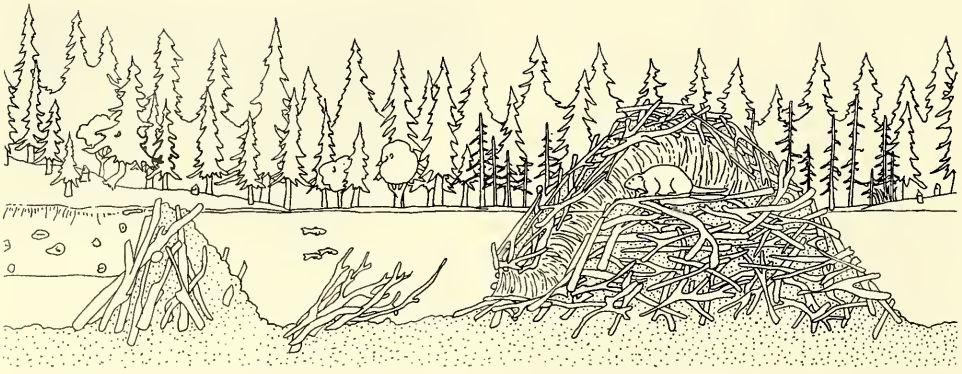


Fig. 39. Typical appearance of a beaver lodge and dam.

ning water apparently serves as the stimulus for such construction activities. Their engineering skills are quite remarkable. Dams are 23–30 m, or more, in length, although some exceed a distance of 0.5 km. They are constructed from a foundation of rocks and mud on which tree limbs are piled. Leaves and mud are then packed around the limbs as mortar. Standing water behind these dams provides the beaver with a pool of water around which to move, provides protection from predators, and serves as a storage site for winter food. Often in association with this pond, are a series of intricate canals that the beaver dig. This aquatic waterway is then used to float vegetation needed for construction of their lodge, the dam, or food cache.

Beavers become active toward late afternoon or evening, foraging and reconstructing dams and lodges throughout the night. In early morning, they retreat to their lodge to rest. They are strict herbivores, feeding on a variety of woody species, and herbaceous aquatic plants. Leaves, twigs, and bark of aspen, cottonwood, willow, and alder are preferred, but conifers may also be eaten. One of the most common signs of beaver activity is fallen trees around a lake or stream that have been chisled through by the beaver's powerful, ever-growing incisors (Fig. 40). Gnawing associated with tree-felling in beavers is required to keep incisors in a sharpened, chisel-like configuration. Lower incisors are rubbed constantly against the inside of the upper incisors to maintain their beveled shape; softer dentine on the inner surface of the tooth, overlane by harder enamel, assures the formation of this shape (Fig. 41).

Trees are felled to provide the animal with a ready source of branches and bark as winter forage. Based on a survey of caches in southeastern Montana, willow is the preferred winter food (Martin 1977; Swenson and Knapp 1980). Other plant materials, particularly roots and rhizomes of water lilies, also have been shown to be important.

During winter, beavers will leave the lodge to recover previously stored caches of branches under the ice. They can stay submerged for up to 15 minutes, although 3–4 minutes is more common. Rarely will they attempt to come out on land during the winter because they are somewhat slow and clumsy, which leaves them vulnerable to predation by wolves and coyotes.

When frightened, a beaver will customarily slap its tail on the surface of the water. This behavior, referred to as a "warning dive," likely not only startles a potential predator but warns other beavers of a possible threat. When this sound is heard, other beavers respond by immediately swimming to deep water. The animal making the tail slap will resurface to swim around the intruder and continue to slap the water. Of-

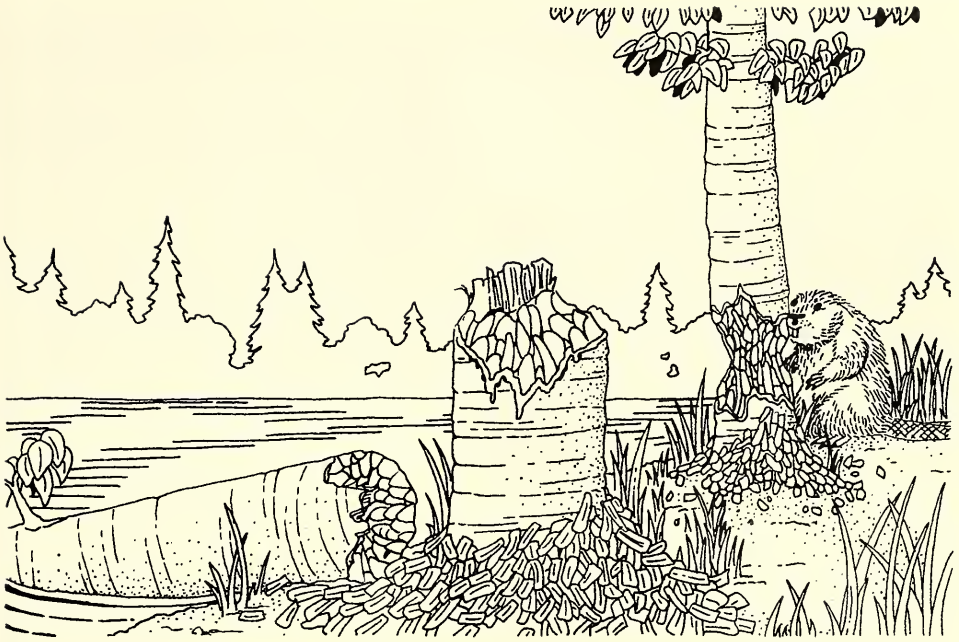


Fig. 40. Typical appearance of trees felled by a beaver.

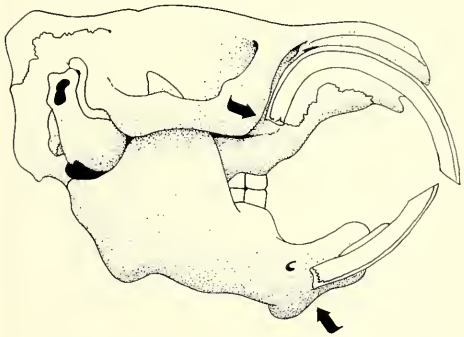


Fig. 41. Chisel-like appearance of incisors and open roots (arrows) in the beaver.

ten beavers can be approached quite closely when this occurs.

Some degree of territorial behavior is exhibited between colonies. Adults mark their environment by excreting oils from 2 pair of glands at the base of the tail: anal glands and castor glands. Beavers mix these oils with mud placed around their territories.

The thick, luscious winter pelt of the beaver nearly became its undoing because of heavy trapping pressure over the past 200 years. In Europe and North America, populations of beavers were trapped to near extinction by the early 1900s. Reestablishment attempts, however, have been so successful throughout the country that extensive harvesting is again permitted. In Montana, 8,620 animals were taken during the 1995–1996 trapping season from 46 of Montana's 56 counties.

Reproduction: Timing of the breeding season of beavers in Montana is unknown. Just to the southwest, in Utah, testicular development reaches its peak between December and March (deRoos 1958), while just north in Saskatchewan maximal spermatogenesis occurs in January–May (Rock et al. 1991). In general, throughout North America peak breeding extends from January to February, with young being born from April to June, after a 107 day gestation. Latitude may influence these dates (Rock et al. 1991), and thus, timing of breeding in Montana should mir-

ror that in surrounding areas. Females are in estrus for 2 weeks during this breeding period; they are monogamous and may mate for life. Litter sizes average 3–4, although habitat quality and winter severity appear to influence breeding potential.

Young are weaned at 6–8 weeks, although they may nurse for an additional month; sexual maturity is reached during the 2nd or 3rd winter.

A typical beaver colony consists of 4–8 individuals; the adult male and female, their young (kits) from the previous year and, in the spring, kits from the current year. Second-year offspring are forced to leave before the birth of a new litter.

Status: Common in riparian areas.

Jenkins, S. H., and P. E. Busher. 1979. *Castor canadensis*. Mammalian Species 120:1–8.

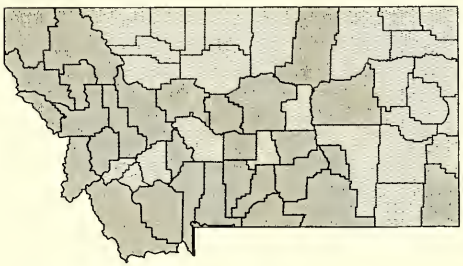
Family Erethizontidae—Porcupine*

Porcupine
Erethizon dorsatum

Fig. 42. Skull of the porcupine (*Erethizon*).

Porcupine (*Erethizon dorsatum*). See plate 4.

Scientific Name: First described by Linnaeus in 1758, and identified as *Hystrix dorsata,* from specimens obtained in eastern Canada. Cuvier appears to have provided this species with its present taxonomic distinction, *Erethizon dorsatum.* The generic designation, *Erethizon,* is from the Greek erithizo, which means "to provoke or excite," and zon, which means "animal." The specific epithet, *dorsatum,* is Latin meaning "back." This name likely refers to the defensive display of the quills along the back when this species is excited.



Map 35. Distribution of the porcupine, *Erethizon dorsatum.*

Description: The porcupine is a medium-sized, stocky animal, with long quills completely covering the dorsal surface. Short legs and tail provide it with a distinctive, rolling gait. Quills are a yellowish-white color, tipped in black or brown. Guard hairs, which are twice as long as the quills, and underfur are highly variable in color, but most often provide a gray to brown cast to the animal. The skull has a large opening immediately in front of the eye socket (Fig. 42). This is the only North American species that possesses quills. This fact alone easily distinguishes the porcupine from all other Montana mammals.

Measurements: [mm(*n*); 2 Wyoming ♀]: TL = ♂ 772.3(5)/♀ 765.7(3); Ta = ♂ 196.3(5)/♀ 214.7(3); HF = ♂ 102.2(5)/♀ 102.0(3); E = ♂ 27(1)/♀ 34.3(3); M [kg(*n*)] = ♂ 8.3(9)/♀ 10.6(3). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The porcupine has a wide distribution across the continental United States, Canada, and Alaska extending into northern Mexico; it is not present in the southeastern United States.

Ecology and Behavior: The porcupine inhabits mixed deciduous–coniferous

* For representative skull characteristics of this taxonomic family refer to Fig. 42.

stands in Montana and prefers areas with a brushy understory for protective cover. They may be found from tundra (Payette 1987) to desert environments. Den sites are chosen in hollow trees, logs, caves, and rock outcrops, and although primarily solitary during most of the year, porcupines may form small groups in winter. Summer diet is quite diverse, consisting of woody roots and stems, herbaceous materials such as leaves and grass, seeds, and flowers. In winter, porcupines forage on the inner cambrial layer of the bark and coniferous needles; cottonwoods, aspens, willows, hemlock, lodgepole, and spruce are preferred (Caras 1967). In hardwood draws of eastern Montana, porcupines prefer American elm, plains cottonwood, skunkbush sumac, and chokecherry (Hendricks and Allard 1988). Porcupines apparently are not only highly flexible in the foods which they can eat but also are highly selective with respect to these foods.

A porcupine may forage on 1 tree for an extended period, girdling and seriously damaging it, but the porcupine's impact on a forest stand is minimal. The porcupine is particularly attracted to salt and wood resins and is often found chewing on everything from sweaty leather boots, and automobile tires to axe handles and plywood structures. Porcupines are nocturnal and active throughout the year. Although they settle down during extreme cold periods, they have been observed active at −30°C.

Yearly movement patterns are highly variable and dependent on local abundance of forage and weather conditions. Animals may range over long distances in spring and summer to find moist sites where succulent vegetation is abundant. At this time, their activity pattern is primarily nocturnal, and their home range may expand to >80 ha (Smith 1975). In winter, they adopt a partly diurnal pattern and their movements may be restricted to a few hectares.

The unique quills of the porcupine can attain lengths of up to 75 mm along the rump and number in excess of 30,000 over the body. The pigmented region of each quill is barbed (Fig. 43). When an attempt is made to remove a quill imbedded in flesh, each barb will flex outward and expose additional, underlying barbs, making removal nearly impossible. The quill shafts are hollow and can be collapsed if cut; this enhances removal, although it is still painful. Nosey dogs and wild animals often find themselves with a snout full of quills (Fig. 44). These must be removed soon because they will continue to work inward. Quills that are lost are replaced in 2–8 months. Damaged quills are routinely replaced during the yearly molt, which begins in midspring and is completed by August.

A porcupine's vision is poor, but they have acute hearing and sense of smell. They are not, by general nature, aggressive, but

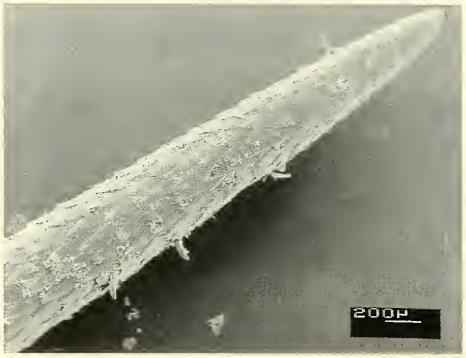


Fig. 43. Appearance of the quill tip illustrating the presence of numerous surface barbs and those underlying each plate (Bar = 200 microns).

Fig. 44. Bighorn sheep after encountering a porcupine.

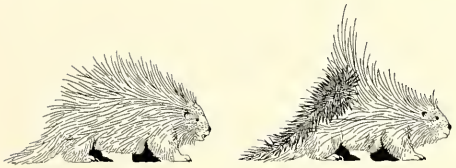


Fig. 45. Normal and defensive stance of the porcupine.

when confronted, they may assume a threatening stance and actually "bluff" charge (Fig. 45). Predators such as the fisher and mountain lion have learned how to roll the porcupine over and attack the soft belly region which is devoid of quills.

Reproduction: The breeding season extends through the autumn in the Northwest. Testicular development and spermatogenesis begin in late August and reach a peak in October. In northeastern Oregon, breeding occurs from October to December (Smith 1977). Females reach sexual maturity at 1.5 years of age. They are seasonally polyestrous, recycling at 25–30 day intervals, after a 8–12 hour estrus if not successfully bred. Gestation lasts for 205–217 days, after which a single young is born, between April and June. Multiple births have been recorded, but are quite rare.

Young are precocious at birth; their eyes are open, and many teeth have ruptured through the gum line. They are fully capable of climbing within a few hours, and their quills harden at this time. Weaning occurs in 4 months (Sweitzer and Holcombe 1993), although young may begin feeding on vegetation within a few weeks. Individuals can live 10 years in the wild.

Status: Common.

Woods, C. A. 1973. *Erethizon dorsatum.* Mammalian Species 29:1–6.

Family Geomyidae—Pocket Gophers*

Idaho Pocket Gopher
Thomomys idahoensis

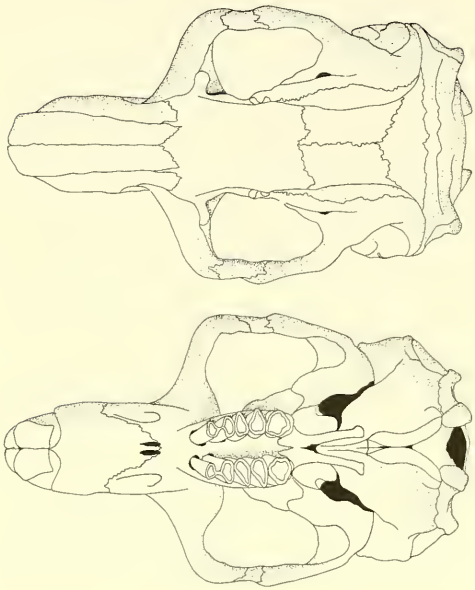


Fig. 46. Skull of the pocket gopher (*Thymomys*).

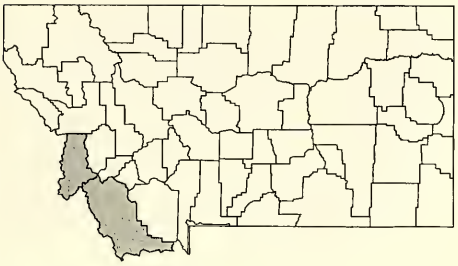
Scientific Name: First described by C. Hart Merriam (1901), as *Thomomys idahoensis,* from a specimen obtained from Clark County, Idaho. Davis (1939) subsequently described this species as a subspecies of *T. talpoides* (*T. talpoides idahoensis*), where it remained taxonomically until a more recent, detailed analysis was provided by Thaeler (1972). Demonstration of reproductive isolation, and resultant maintenance of distinct morphologic and karyotypic characteristics, led Thaeler (1972) to propose species ranking to *idahoensis* again. The generic name, *Thomomys,* is derived from a combination of Greek words, thomos, which means "heap," and mys, which means "mouse." Apparently this was intended to describe a mouse-like mammal that produces mounds (heaps) of earth. The specific epithet identifies the type locality (Idaho).

Description: The Idaho pocket gopher is 1 of 2 species of pocket gophers in Montana. The genus is characterized by external, fur-lined cheek pouches ("pockets"), and extremely long claws on 3 digits of its forefeet. Eyes are small; ears are small and hidden in fur; and incisors are large, recurved, and located outside the mouth cavity. The Idaho pocket gopher is a small species with a somewhat variable color; dorsal surface is yellowish-brown, with hairs variably tipped in dark brown to grayish-brown. The ventral surface is a lighter color, toned with yellowish or yellowish-brown hairs, and the feet are whitish (Thaeler 1972). The tail is short and may be used as a species-specific characteristic. It is difficult to distinguish the Idaho pocket gopher from the other Montana species, the northern pocket gopher, *Thomomys talpoides,* which tends to have a darker, reddish-brown color; black hair patches around the ears (periauricular patches); and a longer tail (Foresman 2001). An analysis of skull characteristics allow positive identification (Thaeler 1972; 1977).

Measurements: [mm(*n*)]: TL = ♂ 195.7(3)/♀ 182.3(8); Ta = ♂ 42.3(3)/♀ 46.0(8); HF = ♂ 23.3(3)/♀ 25.8(8); E = ♂ none/♀ 6.7(3); M [g(*n*)] = ♂ 91.0(5)/♀ 99.1(8). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The Idaho pocket gopher is found sparsely through 5 states: Colorado, Wyoming, Utah, Idaho, and Montana. In Montana, specimens have been

* For representative skull characteristics of this taxonomic family refer to Fig. 46.



Map 36. Distribution of the Idaho pocket gopher, *Thomomys idahoensis.*

collected from Beaverhead County near Dillon and from Ravalli County from Darby to Florence.

Ecology and Behavior: No specific ecological information is available because the Idaho pocket gopher has been considered taxonomically distinct only since 1972. Because the Idaho pocket gopher and northern pocket gopher are very similar morphologically and are sympatric, the Idaho pocket gopher probably resembles the northern pocket gopher in most respects (see account for the northern pocket gopher).

Reproduction: Refer to the species account for the northern pocket gopher.

Status: Locally common.

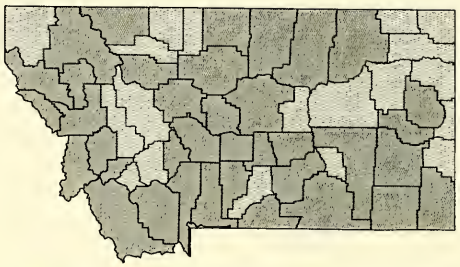
Northern Pocket Gopher
Thomomys talpoides

Northern pocket gopher (*Thomomys talpoides*). See plate 4.

Scientific Name: First described by Richardson (1828) from a type specimen collected near Fort Carlton, on the Saskatchewan River, Saskatchewan. It initially was identified as *Cricetus talpoides*; Baird was 1st to apply current nomenclature in 1858. The generic designation, *Thomomys*, is derived from the Greek combination, thomos, which means "heap," and mys, which means "mouse" (mouse-like animal which makes heaps, a possible reference to the dirt mounds formed during tunnel construction). The specific epithet, *talpoides*, is a combination of the Latin, talpa, meaning "mole," and the Greek contraction, o + eidos, which means "a thing that is like;" "mole-like."

Description: The northern pocket gopher is a small-sized animal possessing unique anatomical characteristics for fossorial life. It has small eyes and ears set deeply into the fur, robust forearms with extremely large claws on 3 digits of its forefeet, and sharply recurved incisors which lie outside the mouth cavity. External, fur-lined cheek pouches lie on both sides of the mouth (from which the vernacular term pocket is derived; Fig. 47). It has a rich, reddish-brown dorsal pelage (although individuals in the eastern region are a lighter shade of brown and possess an orangish to yellowish tint) and a dark gray venter. Hair is silky and soft in quality and relatively short. The northern

Fig. 47. External appearance of the pocket gopher illustrating externally projecting incisors, cheek pouches, and claws of front digits.



Map 37. Distribution of the northern pocket gopher, *Thomomys talpoides*.

pocket gopher is difficult to distinguish from the Idaho pocket gopher. The darker color of the northern pocket gopher and presence of black patches of hair around its ears (periauricular patches) are the most readily noticeable differences. Detailed measurements of various skull features, the tail, and an analysis of chromosome number (karyotype) are required for positive identification (Foresman 2001). Distribution of the northern pocket gopher in Montana (see discussion below) also may readily rule out any confusion with the Idaho pocket gopher.

Measurements: [mm(*n*); ear measurement from Hall 1981]: TL = ♂ 198.4(10)/♀ 198.3(10); Ta = ♂ 61.7(10)/♀ 129.7(10); HF = ♂ 26.4(10)/♀ 26.3(10); E = ♂/♀ 5–6; M [g(*n*)] = ♂ 91.1(10)/♀ 87.9(10). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The northern pocket gopher is distributed across the western half of the United States from the Canadian provinces to New Mexico, westward to California.

Ecology and Behavior: The northern pocket gopher may be found in a variety of habitats, although soil characteristics play an obvious role in local distributions. Deep, loose soil is preferred and explains the relative abundance of this species in higher mountain meadows of the west. To the northeast, northern pocket gophers are found in sagebrush habitat, particularly along riparian zones, but the drier environment keeps population sizes lower. Tryon (1947a) studied the extensive burrow system of this fossorial species, from which this description is derived. A central nest cavity 0.2–0.3 m in diameter is created 0.5 to 0.8 m below the surface, from which 2 or more tunnels radiate out and eventually run just under the surface. Additional chambers are dug from the walls of the deeper tunnels to provide storage space for food, and a blind-ending tunnel is created for fecal deposits (Fig. 48). The nest cavity is filled with shredded vegetation and grass and sits above the entrance tunnels providing drainage. Food chambers are kept filled with roots and other food materials. Forage tunnels, connected to the deeper "shelter" tunnels by spiral segments, are created near the ground surface and may extend for 30 m or more within the root layer. At intervals of 1–3 m, lateral tunnels to the surface are dug to push excavated dirt out of the main tunnel system. These mounds are readily apparent in a meadow and are generally the only indication that northern pocket gophers are present. Northern pocket gophers are solitary throughout much of the year. The burrow system of 1 individual is not thought to connect with that of any other except during the breeding season.

Most activity occurs below ground at dusk and just after dawn as the animal forages on roots, bulbs, tubers, and stems of a large variety of plant species. In Montana, the pre-

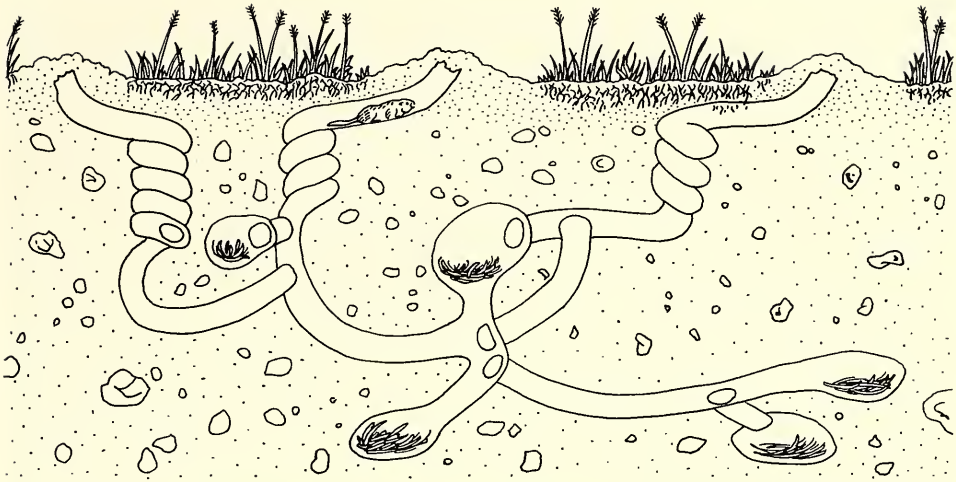


Fig. 48. Diagram of the burrow system of the pocket gopher.

ferred foods are mountain dandelion, onion grass, springbeauty bulbs, the stems and roots of clover, and geranium (Tryon 1947a). Plant materials are cut and, if not eaten immediately, are stuffed inside the cheek pouches where they are carried to storage chambers. Occasionally, an individual gopher will come above ground to forage; this most often occurs during winter when a cover of snow exists. Tunnels created in the snow are filled with dirt from earthen tunnels; when snowmelt occurs in the spring these distinctive dirt casts are left above ground.

Besides the obvious forelimb modifications required for fossorial existence, members of the genus *Thomomys* have highly evolved jaw musculature and procumbent incisors that allow them to dig through the soil with their teeth. This specialization is not found in a 2nd common genus of pocket gopher, *Geomys*, but is particularly advantageous in compact soils. Species of *Thymomys* are thus able to take advantage of a broader range of habitats, including soils with a clay content of >30%. Many other specialized characteristics have evolved to support this lifestyle. Specialized hairs on the face (vibrissae) and tail are sensitive to vibrations and may be used to avoid predation. Hearing also is acute although, as would be expected, vision is poor. Skin is loosely attached to the body, which allows the animal to nearly turn within its skin, making 180° movements in a narrow tunnel possible. Digging behavior is so ingrained in the pocket gopher that when placed within a relatively shallow container, they will attempt to dig until exhaustion, although they could easily climb out.

A single molt occurs in early summer; a molt line appears across the back and moves posteriorly as hair is replaced (Tryon 1947b).

Reproduction: Detailed field reproductive data collected by Tryon (1947a), from a population in the Bridger Mountains of Gallatin County, provide the following account. Male reproductive activity, as indicated by testicular enlargement and spermatogenesis, begins in early March at 1,850–2,300 m, with peak development occurring between March and April. Reproductive activity at lower elevations may begin a month earlier. Breeding begins in mid- to late April, peaking in May, although pregnancies as late as June 24 have been observed. Single litters are produced, averaging 4–5 young. Growth is rapid the 1st summer and migration occurs by late August.

Status: Common and locally abundant.

Verts, B. J., and L. N. Carraway. 1999. *Thomomys talpoides*. Mammalian Species 618:1–11.

Family Heteromyidae—Heteromyids*

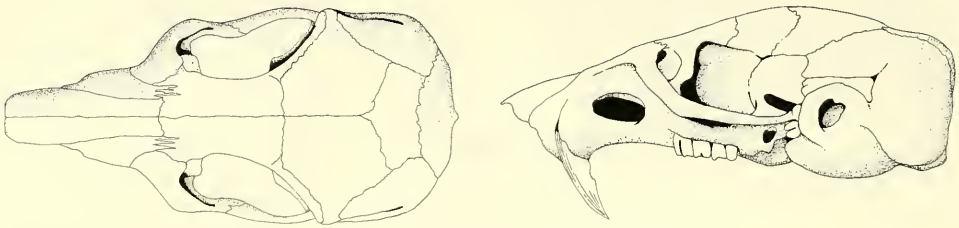
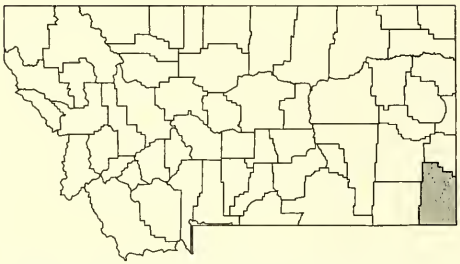


Fig. 49. Skull of a heteromyid (*Perognathus*).

Hispid Pocket Mouse
Chaetodipus hispidus

Scientific Name: First described by Spencer Fullerton Baird, the founder of the United States National Museum (now the Smithsonian), in 1858, from specimens obtained near Tamaulipas, Mexico. Identified initially as *Perognathus hispidus,* the subgenus was elevated to generic status, with the currently accepted name now *Chaetodipus hispidus.* The generic name, *Chaetodipus,* is derived from the Greek combination: chaeta which means "long hair," di meaning "two," and podos, which means "feet." The specific epithet, *hispidus,* is from the Latin, hispidus, which means "spiny or rough;" a direct reference to the spiny bristles on this species' rump.

Description: The vernacular term "pocket mouse," applied to this and 2 other Montana species, denotes presence of external cheek pouches similar to those found in pocket gophers. The pelage of the hispid pocket mouse can best be described as "harsh," with a rump patch of noticeable spiny bristles. Dorsal color of yellowish-orange mixed with black, gives way to a white venter. The well-haired tail has a black stripe down its dorsal surface, and the hind feet are naked. The best way to distinguish this species from other Montana pocket mice is the appearance of its hind feet and texture of its coat. Both species of *Perognathus* possess hairy feet and a soft coat. Also, only the olive-backed pocket mouse is sympatric with the hispid pocket mouse, and the former species is easily distinguished by pelage color.



Map 38. Distribution of the hispid pocket mouse, *Chaetodipus hispidus.*

Measurements: [mm(*n*)]: TL = ♂/♀ 220.0(10); Ta = ♂/♀ 106.6(10); HF = ♂/♀ 26.4(10); E = ♂/♀ none; M [g(*n*)] = ♂/♀ 32.0(7). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: Ranges from North Dakota to central Mexico along a relatively narrow band through the westcentral part of the United States. Only 1 record of this species has been described in Montana (Pefaur and Hoffmann 1971).

* For representative skull characteristics of this taxonomic family refer to Fig. 49.

Ecology and Behavior: In Montana, the hispid pocket mouse has been collected in a mixed grassland community (needlegrass, sedge, broom bluestem, bluestem wheatgrass, blue grama) in association with ponderosa pine stands. South, across the United States, it can be found in a variety of dry grassland habitats, from shortgrass prairie to mid- to tall grass stands. Unlike the olive-backed pocket mouse, the hispid pocket mouse does not depend on sandy soils, being found instead in areas which are more gravelly; soils east of Long Pine Hills in Carter County, where the lone Montana specimen was collected, consist of a sandstone-shale layer over glacial till.

Burrows are constructed in loose soil in areas of moderate grass stands; dense brush is avoided. By nature, the hispid pocket mouse is highly aggressive and solitary. A branched tunnel system is constructed containing food and nest chambers and having as many as 3 openings. Active burrows are readily recognized by presence of a dirt pile near 1 of the openings. Often openings are plugged by soil during the day to be opened as the individuals exit for nocturnal foraging. Seeds make up a large majority of the diet. Sunflower, sagebrush, and bluestem seeds occur in abundance in food storage chambers, as have a large number of other seeds. Insects also are commonly taken. The diet of populations in Montana is unknown.

Although the hispid pocket mouse can hibernate in response to brief cold exposure, or food deprivation, it likely avoids this necessity by subsisting on seed stores. Again no information is available on populations in Montana.

Reproduction: In most regions of the country the hispid pocket mouse produces 2 or more litters/year between spring and late summer. Litter sizes range from 2–9; no other developmental information is available.

Status: Rare.

Paulson, D. D. 1988. *Chaetodipus hispidus.* Mammalian Species 320:1–4.

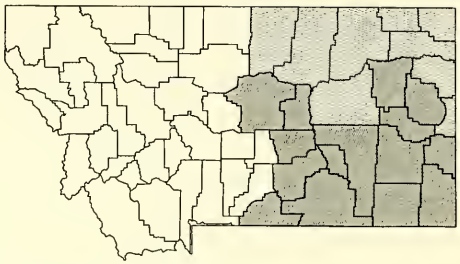
Ord's Kangaroo Rat
Dipodomys ordii

Scientific Name: First described by Samuel Washington Woodhouse, a surgeon and naturalist, in 1853, from specimens obtained in El Paso County, Texas. His taxonomic identification is still held today. The generic distinction, *Dipodomys,* is from the Greek combination, di, meaning "two," podos, meaning "foot," and myos, meaning "mouse;" a reference to the bipedal mode of locomotion exhibited by this species. The specific epithet, *ordii,* honors George Ord, President of the Academy of Natural Sciences of Philadelphia when Woodhouse published his account in the academy's journal.

Description: The Ord's kangaroo rat, as its vernacular name implies, physically resembles a kangaroo, possessing very large hind feet, a moderately strong tail, and small forelimbs (Fig. 50). When moving fast, it adopts a saltatorial (jumping) mode of locomotion, best described as "ricochetal" (bipedal saltation) and similar to that familiar to kangaroos. Color of the dorsal pelage is predominantly a dark cinnamon-buff in Montana. This contrasts sharply with the venter, the hind feet, and 2 patches on the head (supraorbital and subauricular regions), which are pure white. The tail also is bicolored, with white on the sides and ventral surface, and is tipped by a distinct tuft of hairs.

The size and unique physical features of this species precludes confusion with any other rodent in Montana.

Fig. 50. Skeleton and body conformation of the kangaroo rat illustrating the highly modified hindlimbs for richochetal locomotion.



Map 39. Distribution of Ord's kangaroo rat, *Dipodomys ordii.*

Measurements: [mm(*n*)]: TL = ♂ 274.0(3)/♀ 261.3(8); Ta = ♂ 151.3(3)/♀ 153.1(8); HF = ♂ 43.0(3)/♀ 42.4(8); E = ♂ none/♀ 13.6(5); M [g(*n*)] = ♂ 66.1(3)/♀ 63.5(7). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: Thirty-four subspecies of Ord's kangaroo rat are currently recognized and distributed from Alberta and Saskatchewan to central Mexico and from the middle of the United States to Washington, Oregon, and California. Although most range maps indicate that it inhabits the eastern one-half of Montana, specimens have been recorded only from counties in the southcentral to southeastern portions of the state.

Ecology and Behavior The Ord's kangaroo rat is well suited to desert environments exhibiting a wide range of anatomical, physiological, and behavioral characteristics that allow it to live under such harsh conditions. This rat prefers arid regions characterized by sandy friable soils that can be manipulated easily for burrow construction. In several western states, it has been affiliated with juniper and sagebrush-grassland vegetative communities. Burrows are shallow (often no more than 0.2 m under the surface) and contain a nest chamber and several food storage chambers, connected to the surface by long tunnels. Escape holes for immediate access apparently are placed around the central burrow system. Animals retreat to their burrows during the hotter portions of the day to conserve moisture and avoid heat stress.

In common with pocket mice, kangaroo rats are primarily granivorous, preferring seeds of various grasses and forbs. Insects also make up a significant proportion of the diet. The Ord's kangaroo rat's microhabitat affinity, foraging strategy that targets sites of seed abundance, and preference to select seeds based on their size reduce competition with other desert heteromyids. Through nocturnal foraging bouts, the Ord's kangaroo rat gathers seeds in large quantities and stores them in well-developed external cheek pouches for transport back to the burrow. Large caches of seeds are maintained in storage chambers of the burrow system as a hedge against drought conditions. Metabolic production of water from foods and kidneys capable of concentrating urine are highly effective in offsetting the harsh realities of desert life. Activity patterns are influenced by weather conditions. Overcast nights are preferred, because these afford protection from predators and reduce moisture loss; clear, moonlit nights and periods of rain are avoided.

Home-range size varies with season, habitat type, and local seed abundance. On average, males and females use 0.5 ha. Under ideal vegetative conditions populations may rise as high as 53/ha.

One of the most unique anatomical features of the Ord's kangaroo rat is the highly developed middle ear. One of 3 bones of the middle ear, the malleus, is greatly elongated serving as a lever arm to increase the magnitude of sound impulses which impinge on the tympanic membrane (eardrum) and transfer them to the inner ear. Coupled with a significantly enlarged tympanic membrane, the amount of pressure exerted on the fluid of the inner ear is greatly amplified. In concert, these anatomical specializations amplify sound impulses received by the ear by a factor of 97:1. This amplification is greater than 5 times that developed in humans and provides the kangaroo rat with extremely sensitive hearing in the low frequency (1–3 kHz) range. Significantly, within this range, wingbeats of an owl and the sounds produced by a rattlesnake moving across a sandy substrate are heard. Thus, the Ord's kangaroo rat can hear its primary predators as they move in for an attack.

Reproduction: No information is available on the breeding season in Montana. In the more northern extension of its range, it displays 1–2 distinct breeding seasons, extending from January through October. In southern populations, breeding may occur year-round. Two to 4 young are produced after a gestation period of 28–32 days. Sexual maturity is reached in 83 days but young, particularly in northern populations, do not breed until their 2nd year.

Status: Locally common.

Garrison, T. E., and T. L. Best. 1990. *Dipodomys ordii.* Mammalian Species 353:1–10.

Olive-backed Pocket Mouse
Perognathus fasciatus

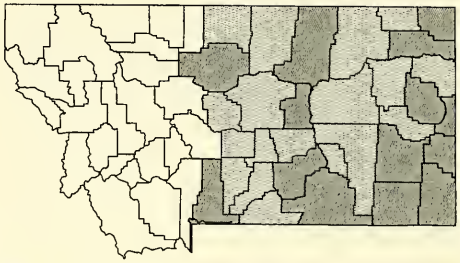
Scientific Name: First described by Maximillian Wied (1839), from a specimen collected near the confluence of the Missouri and Yellowstone rivers in northwestern North Dakota. Wied applied the taxonomic distinction, *Perognathus fasciatus,* which is still accepted. The generic designation, *Perognathus,* is derived from the Greek combination, pera, which means "pouch," and gnathus, which means "jaw;" this is in obvious reference to the cheek pouches of this species.

The specific epithet, *fasciatus,* is Latin for "banded," denoting the lateral, buffy line of color separating the dark dorsal pelage from the white venter.

Description: The olive-backed pocket mouse is the smallest of 3 pocket mice in Montana. As its vernacular name indicates the dorsal pelage is a dark, almost blackish, olive color. The venter, which is white to buff, is separated from the dark dorsal pelage by a bright buffy lateral line. A distinct buffy spot appears just posterior to the ears (postauricular region). The olive-backed pocket mouse can be distinguished readily from the only other sympatric pocket mouse in Montana, the hispid pocket mouse, by its soft pelage and the absence of spiny bristles on its rump. *P. fasciatus* does not occur sympatrically with *P. parvus*; in hand, the former species also can be distinguished by its overall smaller size and olivaceous color.

Measurements: [mm(*n*)]: TL = ♂ 122.5(3)/♀ 141.0(2); Ta = ♂ 59.3(3)/65.0(2); HF = ♂ 16.0(3)/♀ 18.5(2); E = ♂ 8.0(3)/♀ 7.0(1); M [g(*n*)] = ♂ 12.2(5)/♀ 10.9(3). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: This pocket mouse extends from southern Alberta across Saskatchewan to western Manitoba southward across Montana, and the Dakotas to central Colorado. The center of its range lies in the southeastern corner of Montana. It has the largest range in the state of any pocket mouse.



Map 40. Distribution of the olive-backed pocket mouse, *Perognathus fasciatus.*

Ecology and Behavior: The olive-backed pocket mouse, a resident of the Northern Great Plains, prefers arid to semi-arid habitats that are sparsely vegetated. In southeastern Montana, grazed, and ungrazed meadows of shortgrass and sage, characterized by sandy soils, are used. Burrow systems constructed in sandy to clayey soils may extend over distances of 6 m and to depths of 2 m. These tunnel systems contain a nest chamber and several food storage chambers, similar to those described for other heteromyids.

Largely granivorous in its feeding preference, this pocket mouse selects a variety of seeds and grasses for immediate use and for storage. Seeds of knotweed, Russian thistle, tumbleweed, blue-eyed grass, and grasses gaura, needlegrass, and knotweed, have been found in cheek-pouches.

As with the hispid pocket mouse, the olive-backed pocket mouse may enter torpor, particularly in the autumn, although it does not routinely hibernate during winter because it can store adequate quantities of food for use in winter.

Reproduction: Little detailed reproductive information is available. The breeding season across its range likely extends from May to August. Absence of pregnant or lactating females in a June sample and the occurrence of pregnant females and females with placental scars in July suggest that at least 2 breeding periods may occur. Gestation is thought to last 1 month, with an average of 4–6 young/litter.

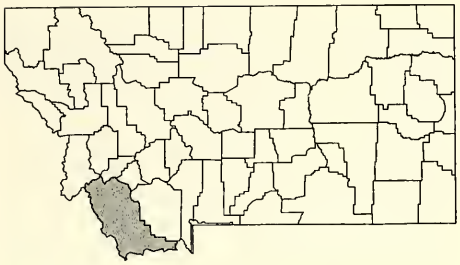
Status: Locally common.

Manning, R. W., and J. K. Jones, Jr. 1988. *Perognathus faciatus.* Mammalian Species 303:1–4.

Great Basin Pocket Mouse
Perognathus parvus

Scientific Name: First described by T. R. Peale (1848), a member of the United States National Museum expeditions of the early 1800s. First designated as *Cricetodipus parvus,* its taxonomic distinction was changed to the currently accepted *Perognathus parvus* by Cassin in 1858. The generic designation, *Perognathus,* is derived from the Greek combination pera, meaning "pouch," and gnathus, which means "jaw;" a reference to the cheek pouches possessed by this species. The specific epithet, *parvus,* is Latin for "little."

Description: The Great Basin pocket mouse is the largest member of the genus and the largest of the pocket mice found in Montana. As a member of the family Heteromyidae, it possesses external, fur-lined cheek pouches. The pelage is soft and, as in other members of the genus, soles of the hind feet are hairy. Color is highly variable



Map 41. Distribution of the Great Basin pocket mouse, *Perognathus parvus.*

even within a population. In general, dorsal pelage is "pinkish-buff to ochraceous-buff, thinly to heavily overlaid with blackish; underparts white to buffy" (Hall 1981:531). A distinctly bicolored tail further distinguishes this species from the olive-backed pocket mouse.

Pelage characteristics and presence of hair on the soles of the hind feet separate the Great Basin pocket mouse from the hispid pocket mouse. Body color distinguishes it from the olive-backed pocket mouse. The Great Basin pocket mouse also is not found sympatrically with the other 2 species.

Measurements: [mm(*n*)]: TL = ♂ 171.3(3)/♀ 157.3(4); Ta = ♂ 93.0(3)/♀ 84.8(4); HF = ♂ 22.0(3)/♀ 20.9(4); E = ♂ none/♀ 4.0(1); M [g(*n*)] = ♂ 15.6(2)/♀ 13.8(3). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: As the vernacular name implies, the distribution of the Great Basin pocket mouse is contiguous with the Great Basin region of the western United States. It ranges through the Columbia Plateau of central Washington into southern British Columbia and eastward across the Snake River Plains of southcentral Idaho to the southwestern corner of Wyoming.

Ecology and Behavior: The Great Basin pocket mouse is a denizen of desert and semidesert habitats dominated by sagebrush and the wheatgrass–bluegrass grassland community, where sandy soils predominate. This holds true for populations in Montana, although 1 site north of Dillon was characterized as being "... almost devoid of vegetation..." (Hoffmann et al. 1969:589). Burrow construction is similar to that of the hispid and olive-backed pocket mice, although burrows generally are shallower (typically 1 m). Nest and food storage chambers are serviced by 2 or more entrances and have the appearance of pocket gopher burrows with soil piled at the openings. "Escape" burrows, simpler in construction than nesting burrows, also are frequently dug in the individual's home range.

Foraging occurs predominantly at night or in the early morning hours. The diet consists of a variety of seeds, predominantly those of grasses, although pigweed and Russian thistle, among other species are eaten. Insects also are eaten, particularly in early spring.

The Great Basin pocket mouse is 1 of the most abundant small mammals in the Great Basin. It is found in close association, and competes with the deer mouse, northern grasshopper mouse, western harvest mouse and, to a lesser degree, the chisel-toothed kangaroo rat (*Dipodomys microps*; a species not found in Montana).

Unlike other pocket mice in Montana that likely remain active throughout the year, the Great Basin pocket mouse hibernates during the colder months. Periodic arousals may allow the animal to feed on stored seeds; the combination of torpor and food storage allows an effective response to variable environmental factors. Interestingly, the pattern of torpor exhibited by members of a population is not synchronized; some individuals may be in torpor while others are active above ground.

As with other pocket mice, the Great Basin pocket mouse is not social. Behavioral trials with other small mammals have demonstrated its aggressive nature, as has their behavior on being handled after capture.

Reproduction: Testicular development begins in February or March and lasts through the summer. Testicular recrudescence apparently is initiated while animals

are still in torpor because males come into breeding condition shortly after emergence. One to 3 litters may be produced annually depending on seasonal conditions. Early and average-to-above average precipitation stimulates vegetative growth and may lead to early reproductive activity. If young are born early enough in the spring, they may reach reproductive maturity and breed by late summer.

Gestation length is probably similar to that of other pocket mice (21–28 days), with mean litter sizes of 3.7–5.5.

Status: Locally common, but only 7 individuals have been collected in Montana.

Verts, B. J., and G. L. Kirkland, Jr. 1988. *Perognathus parvus*. Mammalian Species 318:1–8.

Family Muridae—Murids*

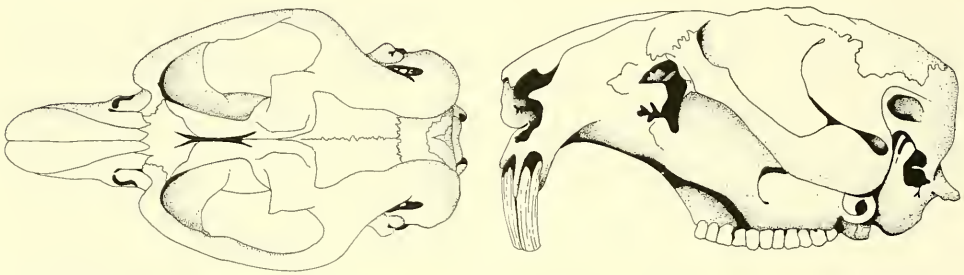


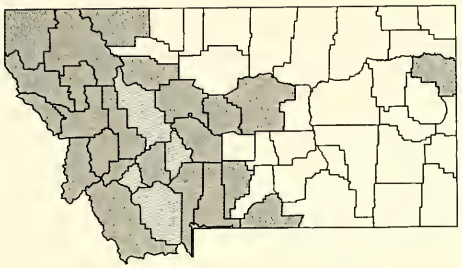
Fig. 51. Skull of a murid (*Ondatra*).

Southern Red-backed Vole
Clethrionomys gapperi

Scientific Name: First described by Vigors in 1830 from specimens obtained between the present city of Toronto and Lake Simcoe, Ontario. The current usage, *Clethrionomys gapperi*, was applied in 1928. The generic designation, *Clethrionomys*, is from the Greek combination kleithrios, meaning "alder wood," and mys, meaning "mouse;" a reference to this species' association with boreal forest habitats. The spe-

Southern red-backed vole (*Clethrionomys gapperi*). See plate 4.

* For representative skull characteristics of this taxonomic family refer to Fig. 51.



Map 42. Distribution of the southern red-backed vole, *Clethrionomys gapperi.*

cific epithet, *gapperi,* was applied in honor of Dr. Anthony Gapper, who collected many mammal species in Ontario in the early 1800s, and in whose essay Vigors appended his description of this species.

Description: As the vernacular name implies, the southern red-backed vole is easily identified by the wide reddish to reddish-brown band of hairs that runs along its dorsal surface from head to rump. This band offsets an otherwise gray dorsal and lateral pelage, which blends to a silvery-white on the venter. General body configuration is that of a vole, however, the ears are much more noticeable than in species of *Microtus.* Unlike other vole species present in Montana, the molariform teeth of the southern red-backed vole are rooted rather than evergrowing.

Measurements: [mm(*n*)]: TL = ♂ 140.7(10)/♀ 137.9(10); Ta = ♂ 40.3(10)/♀ 38.7(10); HF = ♂ 18.5(10)/♀ 17.6(10); E = ♂ 15.0(4)/♀ 14.0(5); M [g(*n*)] = ♂ 24.9(10)/♀ 23.3(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The southern red-backed vole ranges across the Canadian provinces from coast to coast, with southern extensions through the western United States to Arizona and New Mexico. Distributions along the northern tier states extend into New England and southward along the Appalachians into Tennessee and North Carolina.

Ecology and Behavior: The southern red-backed vole is associated with moist densely-forested environments in Montana. The forest understory where it occurs, is most often covered with mosses and ferns; dead and decaying logs are preferred. This complex ground structure provides protective cover and food. Nests are constructed in available cavities under dead trees and their root masses. Abandoned nests of other species also may be used. Grass, leaves, and moss are used as nesting materials.

This species is semifossorial (lives partly under ground) and active year round. Association between ground cover and movement patterns are tight. This vole rarely ventures away from downed woody vegetation, preferring to run along and under these structures. When the animal gets to the end of 1 log, it takes the shortest route possible to again acquire protective cover.

During winter, animals remain active under snow primarily exhibiting a diurnal pattern. They are easy prey for owls as they move through tree wells free of snow on their foraging bouts. In summer they are more nocturnal.

The diet is quite diverse. Although primarily herbivorous, insects and other invertebrates are eaten. Green vegetation, lichens, ferns, mosses, seeds, and berries are highly preferred. This vole also is thought to be integrally involved in dispersal of mycorrhizal fungi throughout the forest. Fungal spores of hypogenous (underground) species that are consumed are carried in the digestive tract as the animal travels on the forest floor. Later, they are expelled in feces; this dispersal greatly enhances propagation of these symbiotic fungi and perpetuates forest characteristics associated with older-aged stands.

This is 1 of the most common voles in the forested regions of the state. Although abundant, population cycles frequently associated with other vole species, such as the meadow vole and sagebrush vole, are not seen in the southern red-backed vole. Normal increases in a local population, which

occur in the late summer and early autumn, as a result of breeding success, are tempered during the winter months through natural mortality.

Reproduction: Breeding begins in March and continues throughout the summer and early autumn. A gestation period of 17–19 days is quickly followed by a postpartum estrus, thus females are capable of producing 2–3 litters each year. Litter sizes range from 5–7. Young begin weaning at the relatively early age of 12–13 days, eating solid food by day 14. Sexual maturity is reached within 3 months with a percentage of young-of-the-year reproducing before their 1st winter.

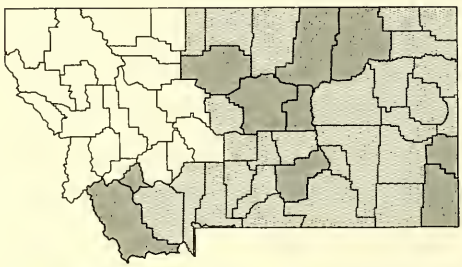
Status: Common, particularly in the west.

Merritt, J. F. 1981. *Clethrionomys gapperi.* Mammalian Species 146:1–9.

Sagebrush Vole
Lemmiscus curtatus

Scientific Name: The sagebrush vole was first described, in 1868, by Edward D. Cope, a noted paleontologist and comparative vertebrate biologist, in whose honor the journal *Copeia* was named. Cope based his descriptions on specimens obtained at Mt. Magruder, Nevada, near the California border. The initial taxonomic name, *Arvicola curtata,* was changed to *Lagurus curtatus* by Thomas, in 1912, and remained as such until a more in-depth revision was completed in 1984. Subsequently, the sagebrush vole is now recognized as *Lemmiscus curtatus* (Carleton and Musser 1984). The generic designation, *Lemmiscus,* is derived from the New Latin combination, lemmus, which means "lemming," and the suffix -iscus, which denotes possession. The specific epithet, *curtatus,* is Latin for "shortened;" a reference its extremely short tail.

Description: The sagebrush vole is a medium-sized vole characterized by its pale, buffy-gray, dorsal color; paler sides; and a silvery-white to buffy venter. The feet are white to light gray and heavily furred. The very short tail, which is about the same size as the hind foot, is slightly bicolored, dusky above and white below. The combination of light coat color and extremely short tail clearly distinguish this species from other



Map 43. Distribution of the sagebrush vole, *Lemmiscus curtatus.*

Montana murids. The bog lemming also has a short tail, but its color is much darker, and its habitat affinities are quite different. All other murid rodents in Montana have longer tails and at least some areas of darkened pelage.

Measurements: [mm(n)]: TL = ♂ 120.0(2)/♀ 120.0(3); Ta = ♂ 23.5(2)/♀ 20.0(3); HF = ♂ 17.5(2)/♀ 17.0(3); E = ♂ 9.5(2)/♀ 10.7(3); M [g(n)] = ♂ 24.2(5)/♀ 26.3(4). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: Sagebrush voles extend from the southern regions of Alberta and Saskatchewan across portions of the central and northern Great Plains westward covering most of the Great Basin. Although rel-

atively few individuals have been collected in Montana, the sagebrush vole may occur east of the Continental Divide wherever suitable habitat exists.

Ecology and Behavior: As its vernacular name implies, the sagebrush vole is an inhabitant of sagebrush communities. It is found in semi-arid environments, in topography ranging from open prairies to narrow, brushy canyons. Besides sagebrush, a ground cover of crested wheatgrass, or rabbitbrush, are important habitat components. An elaborate burrow system, containing as many as 30 entrances, is constructed under, or near sagebrush cover. These burrows may be up to 46 cm in depth. A central nest chamber, accessed by several entrances, is lined with leaves and stems. The sagebrush vole lives in male-female pairs (Hofmann et al. 1989; Mullican and Keller 1986), although earlier suggestions of coloniality have not been ruled out.

Although a strict vegetarian, the sagebrush vole nevertheless has generalized food preferences. Numerous grasses, notably cheatgrass, wheatgrass, bluegrass, and needlegrass are eaten, and leaves and terminal branches of sagebrush, and rabbit-brush. The flowers, bulbs, and seeds of many plants are also used.

The sagebrush vole is active throughout winter foraging along tunnels constructed under the snow. The runway systems, so distinctive of *Microtus,* are not as well defined for the sagebrush vole because ground cover is absent in their preferred habitat.

Populations fluctuate markedly from 1 year to the next. Mild winters followed by moist summers appear to precipitate population increases.

Reproduction: The breeding season of the sagebrush vole appears to be tightly associated with the availability of green vegetation. In the southern extension of its range it may breed throughout the year, while in more northern regions breeding may occur from March through December. A lull in breeding may occur during either dry summers or wet winters.

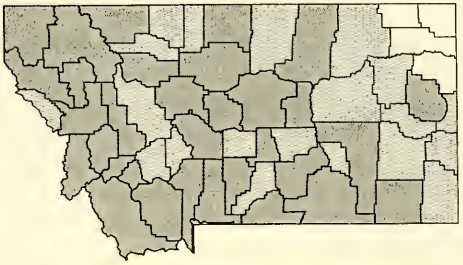
After a gestation of 25 days, an average of 4–6 young are born. Females have a postpartum estrus within 24 hours of birth and thus can produce >1 litter quickly. Three or more litters may be produced annually; lab-raised individuals have successfully produced 6 litters. Young, weaned between days 17 and 25, reach sexual maturity rapidly; females may breed by day 60, while males come into breeding condition between day 60 and day 75.

Status: Uncommon.

Carroll, L. E., and H. H. Genoways. 1980. *Lagurus curtatus.* Mammalian Species 124:1–6.

Long-tailed Vole
Microtus longicaudus

Long-tailed vole (*Microtus longicaudus*). See plate 5.



Map 44. Distribution of the long-tailed vole, *Microtus longicaudus.*

Scientific Name: The long-tailed vole was first described by C. Hart Merriam, in 1888, from specimens collected from Custer, South Dakota. Initially designated as *Arvicola longicaudus,* it underwent numerous taxonomic revisions until Vernon Bailey took an in-depth look at this group and arrived at the generic designation of *Microtus.* This term is from the Greek combination mikros, which means "small," and otos, which means "ear;" the specific epithet, *longicaudus,* is from the Latin combination longus, which means "long," and *cauda,* which means "tail."

Description: The long-tailed vole, as with other voles, has a robust, thick body. It is a small species with a tail greater than one-third its total length (the best distinguishing characteristic, and from which its vernacular name is derived). Dorsal color is quite varied, ranging from the most common dark brown to lighter shades of grayish-brown; black tipped hairs are distributed through the pelage. The sides and venter are more grayish and can become whitish on the belly surface. The tail is distinctly bicolored. Large, well-haired ears are easily observed. The long tail characteristic of this species readily distinguishes it from 2 closely related microtine species, the montane vole and meadow vole. In addition, its smaller size can be used to distinguish the long-tailed vole from the water vole.

Measurements: [mm(*n*)]: TL = ♂ 165.4(10)/♀ 165.4(10); Ta = ♂ 56.7(10)/♀ 57.2(10); HF = ♂ 19.1(10)/♀ 20.0(10); E = ♂ 13.7(6)/♀ 10.5(2); M [g(*n*)] = ♂ 31.7(10)/♀ 31.9(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The long-tailed vole is common throughout the western United States, Canada, and Alaska. It ranges from the Pacific Coast to Montana, southward to New Mexico.

Ecology and Behavior: The long-tailed vole occupies a wide variety of habitats typical of the boreal forest zone, from higher elevation spruce-fir forests and subalpine meadows to more open, lower elevation meadows and riparian zones. It extends as well into open grassy and even sagebrush areas. It avoids old-growth stands, habitat more appropriate for the meadow vole, but invades disturbed sites, such as clear-cuts, following logging activities.

The diet consists of grasses, seeds, and fruit of a variety of plants. In moist forests containing rich humus, the hypogeous fungus *Endogone* is a major component of the diet, particularly in late summer to early autumn when the fungus is abundant. The long-tailed vole, which is nocturnal and active year-round, does not produce well-de-

fined runways in vegetation, a trademark of the meadow vole. Although sympatric with the montane vole, the long-tailed vole seems to be displaced when the montane vole population is on the rise. A 3-year population cycle occurs in concert with that of the montane vole, however, the amplitude of the population change is less.

Reproduction: The breeding season has not been defined for populations in this state. Pregnant females were collected in Idaho from early May into late September and juveniles were seen throughout the summer, indicating that more than 1 litter may be produced (Davis 1939). Multiple litters (range 1–4) occurred for populations in southwestern Alberta (Loewen 1985). Litter sizes average 4–7. Since the lifespan is no longer than 1 year, males and females only contribute to population growth during their 1st, and only, summer as adults. However, if born early in the breeding season, young may become reproductively active their 1st summer (Loewen 1985).

Status: Common and locally abundant.

Smolen, M. J., and B. L. Keller. 1987. *Microtus longicaudus.* Mammalian Species 271:1–7.

Montane Vole
Microtus montanus

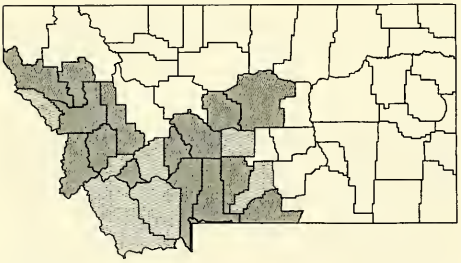
Scientific Name: The montane vole was first described by Titian R. Peale (1848), from specimens obtained near Mt. Shasta, Siskiyou County, California. Originally identified as *Arvicola montana,* the present name was applied by Trouessart in 1897 (Hall 1981:798). The generic distinction, *Microtus* is from the Greek combination mykros, which means "small," and otus, which means "ear." The specific epithet is from the Latin, montanus, which means "of mountains."

Description: The montane vole exhibits the classic vole body form and possesses a short (<50% of body length), bicolored tail; reduced ears hidden in the fur; and a grayish-brown dorsal pelage color. Ventral pelage is white to grayish. The montane vole, at 1st glance, can be easily confused with 2 closely related microtines, the meadow vole and long-tailed vole. The most definitive means of separating the montane vole from the former species is through dental cusp patterns (Foresman 2001). Habitat preferences are useful; the montane vole is more commonly found in drier grasslands, whereas the meadow vole is more closely associated with wet meadows. However, the montane vole will readily inhabit marshes and wet meadows at higher elevations in the absence of the meadow vole. Careful measurement of the tail should distinguish the montane vole from the latter species; however considerable habitat overlap occurs between these species. Although the montane vole is often sympatric with the water vole, the considerably larger size of the latter should clearly distinguish the 2.

Measurements: [mm(*n*)]: TL = ♂ 145.5(10)/♀ 139.2(10); Ta = ♂ 36.7(10)/♀ 34.9(10); HF = ♂ 18.6(10)/♀ 18.1(10); E = ♂ 13.0(1)/♀ 12.5(8); M [g(*n*)] = ♂ 34.4(10)/♀ 30.5(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: Extends from central British Columbia across Washington, Idaho, and Montana, forming a band from California to Colorado. Populations are also found in New Mexico and Arizona.

Ecology and Behavior: As the vernacular name implies, the montane vole is primarily associated with mountainous re-



Map 45. Distribution of the montane vole, *Microtus montanus.*

gions, occurring throughout a variety of habitats in the southwestern quarter of Montana. Research in the Bridger Mountains north of Bozeman illustrated that montane voles occupy a much broader range of habitat types than meadow voles (Hodgson 1970). The montane vole is often found in dry grasslands, particularly those at higher elevations in association with alpine tundra. Here, if the meadow vole is absent, the montane vole will spread into wetter meadows and marshes interspersed within forested areas. The montane vole is less abundant in lower level grasslands of the foothills and plains, a region inhabited primarily by the prairie vole. Such segregations may arise through competitive exclusion (Findley 1954). In the Bridger Mountains the montane vole is behaviorally dominant to the meadow vole (Stoecker 1972). However, dominance in the field is "... probably determined by the relative abundance of each species" (Stoecker 1972:327).

A nocturnal activity pattern is prominent during summer, shifting to a more diurnal pattern in winter (Rowesmitt 1981). The montane vole uses underground tunnels extensively, and above-ground runways. Such systems are complex with many branches servicing feeding areas and waterways (Wolff 1985). Nests may be constructed either above ground or below, but those used for raising litters are always underground (Jannett 1978; 1981). Grass is used exclusively to form a cup-shaped nest (Maser and Storm 1970), which is serviced by 2 entrances (Jannett 1982).

The social structure is a facultative monogamy; dispersion of adults in the population is such that only 1 male is found near 1 female. Under these conditions, a pair bond is formed, but it is neither strong nor is any significant paternal investment made towards the offspring (Jannett 1982). Nests are not shared at any point during the year.

The montane vole is a herbivore. Microtine rodents eat both monocotyledons and dicotyledons, the preferences and amounts of which depend on season and local abundance (Batzli 1985). Fungi and seeds may also be used in autumn and winter when green vegetation is unavailable.

The montane vole may exhibit population fluctuations on a multi-annual basis (Negus et al. 1977), although such fluctuations may not occur in populations from alpine environments (Pattie 1967). The montane vole does not have population cycles of the same magnitude as those of the meadow vole.

Reproduction: The breeding season extends nearly year-round beginning in February and continuing into December (Ferris 1971). Winter breeding occurs, particularly in populations which are expanding (Negus et al. 1977). As in other microtines, gestation is 21 days long, with a post-partum estrus occurring within 24 hours. Litter sizes range from 2–10, with means of 4.08 in Washington (Wright 1971) and 6.32 in Wyoming (Negus et al. 1977).

Rapid attainment of sexual maturity after weaning (Negus and Pinter 1965), male-induced acceleration of reproductive maturity (Sawrey and Dewsbury 1991), and the post-partum estrus contribute to allow pregnancy rates to approach maximal limits. Also, various plant compounds eaten by voles during spring greenup stimulate reproductive activity (Berger et al. 1981; Sawrey and Dewsbury 1991).

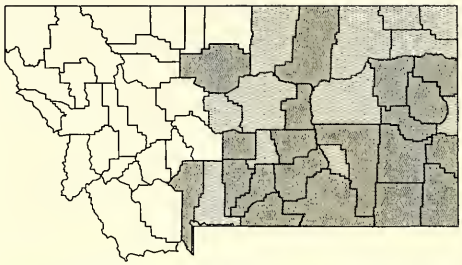
Status: Common.

Prairie Vole
Microtus ochrogaster

Scientific Name: The prairie vole was first described by Schreber in 1842, based on specimens thought to be collected from New Harmony, Posey County, Indiana. The initial scientific designation, *Hypudaeus ochrogaster*, was redefined by Joel Asaph Allen in 1898, to the currently accepted *Microtus ochrogaster*. The generic designation, *Microtus*, is from the Greek combination mikros, meaning "small," and otos, which means "ear." The specific epithet, *ochrogaster*, comes from the Greek combination ochra, which means "yellow-ochre," and gaster, which means "belly," a reference to its ventral color.

Description: The prairie vole is 1 of 4 species in the genus *Microtus* found in Montana of a similar body size and color. Its dorsal pelage is most often grayish-brown, with many hairs tipped in black or brownish-yellow. Hair along the sides is lighter gray, with the ventral surface ranging from whitish-gray to pale cinnamon or yellow-ochre (from which its specific epithet is derived). Tail is distinctly bicolored. Ears and eyes are small in comparison to its large head. The prairie vole can be difficult to distinguish from other *Microtus* in Montana. The slightly shorter tail length of the prairie vole is 1 of the primary characteristics which can be used, although this parameter varies within each species (Foresman 2001). The gray, grizzled, dorsal appearance and yellowish belly separates the prairie vole from other *Microtus* which are more often browner above and grayer below. Additionally, the prairie vole is a denizen of the open prairie, particularly in Montana, a habitat preference which, when used in combination with physical characteristics, may distinguish it.

Measurements: [mm(*n*)]: TL = ♂ 150.2(10)/♀ 149.6(10); Ta = ♂ 32.8(10)/♀ 34.5(10); HF = ♂ 19.1(10)/♀ 18.8(10); E = ♂ 11.9(7)/♀ 12.6(10); M [g(*n*)] = ♂ 44.1(10)/♀ 37.3(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.



Map 46. Distribution of the prairie vole, *Microtus ochrogaster*.

Distribution: The prairie vole extends from central Alberta and central and southern Saskatchewan, across the southern region of Manitoba, to northern New Mexico and Virginia.

Ecology and Behavior: As its vernacular name implies, the prairie vole is primarily associated with grassland prairies. It has, however, been found in riparian grasslands sympatric with the meadow vole. Where this sympatry arises, the prairie vole is restricted to drier habitats. The montane vole is also a dry, grassland species but, where sympatric, it is most often found at higher elevations. Prairie voles are more fossorial than other voles in the state, constructing burrows from which they forage. Several burrows lying 5 cm underground connect to a nest chamber 10 cm deep, with additional, smaller feeding chambers spread throughout. The presence of prairie voles in an area is easily noted by the extensive and well-traveled runway system which they use.

Voles forage day and night, clipping green vegetation to obtain the succulent leaves; grasses, forbs, and sedges are preferred foods. Cuttings that are not eaten are left in the runway system, and can be used to determine vole activity. A diverse array of vegetation is eaten; 79 species of prairie

plants are readily consumed. In autumn, as green vegetation disappears, foraging activity shifts to fruits, seeds, roots, and tubers of diverse plants. Insects are also an important component of the diet. The prairie vole, like many burrowing small mammals, caches a large volume of food for winter use. Materials stored include various grasses and an abundance of seeds and fruits. The prairie vole is also known for the damage which it can cause to tree plantings as it feeds on the bark. Coniferous and deciduous trees are affected.

Some populations have wide numerical fluctuations, although not nearly as pronounced as those for the meadow vole. In the Midwest, cycles are 2- to 4-years long and peak levels may be over 1,000 individuals/ha. However, a 14-year study in eastcentral Illinois failed to identify distinct, multiannual population fluctuations. Probably fluctuations are the result of local abiotic factors, annual moisture and resultant plant growth for example, rather than an intrinsic mechanism.

The prairie vole is an aggressive species capable of dominating, or displacing, others. Intraspecific aggression during the breeding season is also well-documented (Rongstad and Gaines 1976). A monogamous relationship develops between a breeding pair. Social organization consists of communal groups; the male–female pair serves as the nucleus to which their young, and other unrelated adult individuals, are added (Getz et al. 1993). These communal groups can exist throughout the year, but are most common during autumn and winter (Getz et al. 1993).

Reproduction: Reproductive activity probably extends throughout the year, although a reduction may occur in December and January. Breeding peaks are tied closely to available moisture, no doubt as this relates to green vegetation and the stimulatory reproductive effects of this plant material (Sawrey and Dewsbury 1991). After a gestation of 20–22.8 days, an average of 3.5 young are born. Females reach sexual maturity by day 40, males between 49 and 60 days. Post-partum estrus occurs, and prairie voles can be particularly prolific. Mortality is so high, however, that realistically only 1 or 2 litters are commonly produced.

Average lifespan in the field is 1 year.

Status: Common.

Stalling, D. T. 1990. *Microtus ochrogaster*. Mammalian Species 355:1–9.

Meadow Vole
Microtus pennsylvanicus

Meadow vole (*Microtus pennsylvanicus*). See plate 5.

Scientific Name: The meadow vole was first described by George Ord, a naturalist and co-founder of the Academy of Natural Sciences of Philadelphia, in 1815, from specimens obtained near Philadelphia, Pennsylvania. The vernacular name is derived from this occurrence. Initially designated *Mus pennsylvanicus*, the taxonomic distinction was changed to the current usage in 1895. The generic designation, *Microtus*, arises from the Greek combination mikros, meaning "small," and otus, meaning "ear." The specific epithet, *pennsylvanicus*, is a Latinized term for the type location.

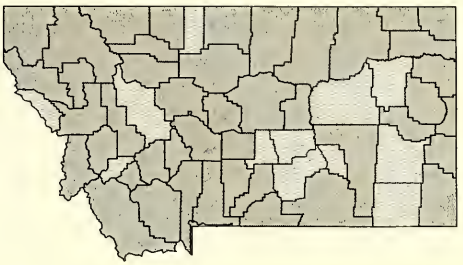
Description: One of 4 nearly equally-sized species of *Microtus* in Montana, the meadow vole is similar in many additional respects to these other forms. Dorsal color varies widely from a yellowish-chestnut to a dull, dark brown tipped with black between populations across its entire range. In Montana it is most often the latter. Ventral surface is grayish. Tail is bicolored with dark brown above and grayish below. Six plantar tubercles (foot pads) are present and diagnostic.

The darker color of the meadow vole is the best characteristic available to distinguish it from the montane vole in hand. For confirmation, a detailed analysis of the dental cusp pattern is required (Foresman 2001). It can be separated from the long-tailed vole and prairie vole by tail length (Foresman 2001).

Measurements: [mm(n)]: TL = ♂ 143.3(10)/♀ 149.4(10); Ta = ♂ 34.4(10)/♀ 36.6(10); HF = ♂ 20.0(10)/♀ 18.1(10); E = ♂/♀ 12–16; M [g(n)] = ♂ 29.7(10)/♀ 32.2(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: More widely distributed in North America than any other species in the genus *Microtus*. The meadow vole ranges from Alaska, to Nova Scotia, and across the northern continental United States, dipping into Georgia and South Carolina. Disjunct populations occur in the southwest and Mexico. It is found throughout Montana preferring lower elevation, wet grassland habitat. In the northwestern corner of the state, it may occupy drier grasslands if adequate cover is available, and if the montane vole is absent. Populations may extend to treeline and are found along streams and within moist meadows in forested areas, but are absent from alpine regions.

Ecology and Behavior: The meadow vole is less fossorial than the prairie vole, a fact due in part to its use of moist habitats. Since it often cannot burrow into the waterlogged soil, its nests are constructed above ground in dense grass cover. Nests are round in shape formed from leaves and stems, with an inner lining of finely shredded plant material. Distinct runways along the ground in dense cover are a sure sign of the meadow vole's presence; runways may be abundant, particularly during population peaks.



Map 47. Distribution of the meadow vole, *Microtus pennsylvanicus*.

The herbaceous diet of the meadow vole is quite broad with over 70 species of plants eaten. Graminoids such as bluegrass, muhlenbergia, old-witchgrass, and bluestem predominate in the diet. In winter, animals shift to seeds, roots, hypogeous fungi (*Endogone*), and insects. In Montana, the meadow vole damages fruit trees during periods when its populations are high. Trees in an orchard can be so severely girdled that they are irreparably damaged. Active year-round, the meadow vole does not cache food as does the prairie vole.

Cyclic variations in population size are routine for this species and occur at 2- to 5-year intervals. Although food quality and abundance, climatic factors, predation, and stress brought on by increasing numbers may drive the cycles no completely satisfactory explanation is currently available (Krebs 1996).

Long distance dispersals are common for meadow voles. These movements are in part driven by overall population densities, but may also be influenced by restrictions in the preferred meadow habitat and lack of maternal interest in juveniles. Juveniles, abandoned shortly after weaning, disperse and look for available habitat to acquire. Ex-

tremely high mortality in such dispersers, in excess of 88%, makes the 1st month of life tenuous. Even if an individual survives this initial period, so many predators exist (in the form of snakes, hawks, owls, and weasels) that life expectancy, after attaining sexual maturity, is only 6–10 months.

Communal nesting occurs during winter (Madison et al. 1984). Such aggregations obviously impart metabolic savings to these individuals.

Reproduction: The meadow vole can breed throughout the year. Most activity occurs between March and November, but breeding can continue into winter if snow cover is heavy enough to provide an insulating barrier (Jones et al. 1983). Consumption of green vegetation, particularly seedlings, stimulates reproductive activity (Sanders et al. 1981). Gestation lasts 21 days; average litter size is 3.78–6.2, although this is highly variable depending on season, weather conditions, and latitude. Young are weaned between days 10 and 14 and may reach sexual maturity 2–3 weeks later (Jones et al. 1983). Female reproductive development can be activated by airborne chemical stimuli (pheromones) emitted by males (Baddaloo and Clulow 1981). Pregnant females may abort when exposed to chemical cues produced by unfamiliar males, a phenomenon referred to as the "Bruce effect" (named for H. M. Bruce who first described this situation).

Females exhibit a post-partum estrus thus, if they survive (see comments above), they can be highly prolific. No social structure exists as in the prairie vole; adults are promiscuous (Madison 1980).

Status: One of the most common mammals in Montana.

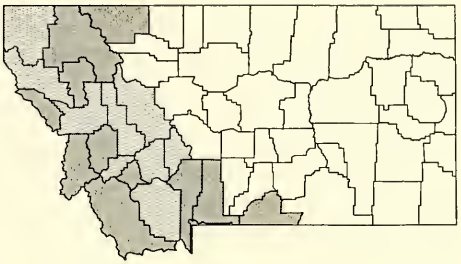
Reich, L. M. 1981. *Microtus pennsylvanicus*. Mammalian Species 159:1–8.

Water Vole
Microtus richardsoni

Water vole (*Microtus richardsoni*). See plate 5.

Scientific Name: The water vole was first described by J. E. DeKay, in 1842, from a specimen obtained near Jasper House, Alberta, Canada. Originally designated as *Ar-*

vicola richardsoni, the water vole has since been placed in the genus *Microtus.* The generic designation *Microtus* is derived from the Greek combination mikros, which means "small," and otus, which means "ear." The specific epithet, *richardsoni,* honors J. Richardson, an early 1800s naturalist, who described many specimens collected during Sir John Franklin's expedition to the northwest between 1818 and 1822.



Map 48. Distribution of the water vole, *Microtus richardsoni.*

Description: The water vole is the largest vole in the state and 1 of the largest, wild murids; only the muskrat and bushy-tailed woodrat are larger. Water voles in Montana are most commonly dark brown to reddish-brown, tipped in black, although the pelage has a grayish cast in some populations. The ventral surface is lead gray with an overall white cast. Tail is bicolored: dark brown above and gray below. Two distinguishing characteristics are large hind feet [>22 mm] and noticeably protruding incisors. Overall body size (on average twice as large as other voles) and vole-like confirmation, clearly distinguish this species from all others within its range.

Measurements: [mm(*n*)]: TL = ♂ 238.5(10)/♀ 219.3(10); Ta = ♂ 76.4(10)/♀ 72.6(10); HF = ♂ 25.9(10)/♀ 25.8(10); E = ♂ 16.9(8)/♀ 15.0(7); M [g(*n*)] = ♂ 112.7(10)/♀ 100.0(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The water vole is restricted to northwestern North America in 2 distinct regions: a band from southern British Columbia along the western portions of Washington and Oregon and secondly from eastern British Columbia and Alberta through the eastern borders of Washington and Oregon, and encompassing portions of Idaho, Montana, Wyoming, and Utah.

Ecology and Behavior: As its vernacular name implies, the water vole is found near water, particularly streams and pond systems in alpine and subalpine regions. They prefer high elevation, aquatic habitats which are often small and fragmented. The distribution of the water vole in such habitats was influenced by glacial events over the past 18,000 years. Originally adapted to tundra conditions, the water vole moved northward in direction and upward in elevation into montane habitats as the Cordilleran Ice sheet receded, about 18,000 to 10,000 years ago. Other species' distributions in Montana (e.g., northern bog lemming) resulted from similar geological changes.

Burrow systems of the water vole are constructed just beneath the root layer, along stream banks. An elaborate tunnel network provides immediate access not only to the stream, but to foraging areas and the nest chamber itself. Additionally, short, subterranean segments are used as resting sites and protected feeding areas. Nests, constructed of cuttings from aquatic plants [e.g., rushes and sedges], typically fill a chamber 10 by 10 by 15 cm in dimension.

Water voles are active year-round when snow levels accumulate, subnivean tunnels are constructed which allow individuals to feed without coming to the surface. Water voles do not hoard food for winter use. The diet consists of a variety of aquatic herbaceous vegetation, from grasses and sedges to more woody materials such as willow stems. Huckleberry leaves and the bulbs of the glacier lily are eaten, as are roots of willow, lousewort, arnica, and glacier lily.

Reproduction: In southwestern Alberta the breeding season extends for 3–3.5 months, from mid-to-late May to early Sep-

tember (Ludwig 1988). Gestation is 22 days and females have a post-partum estrus within 24 hours of parturition. Ovulation is induced by copulation. Gestation is not longer when females are simultaneously pregnant and lactating. Adult females produce 1 or 2 litters during the summer, with a mean litter size of 5 (2–9). This lower reproductive output seems to prevent large population fluctuations characteristic of other microtine species (Ludwig 1988). This microtine, which exhibits all of the reproductive phenomena appropriate for a high reproductive output, actually produces very few young. Plant compounds may restrict reproductive activity in these habitats (Ludwig 1988).

Young are weaned by 21 days; evidence of male reproductive activity has been observed by day 60. A low percentage of individuals (~ 26%) can breed during the 1st summer of life, likely those born earliest in the breeding season. This, and the fact that adult mortality is so high, contributes to a low reproductive output for the population as a whole.

Status: Uncommon and tightly restricted to small, fragmented habitats.

Ludwig, D. R. 1984. *Microtus richardsoni.* Mammalian Species 223:1–6.

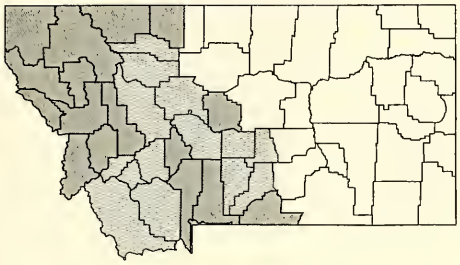
Heather Vole
Phenacomys intermedius

Scientific Name: The heather vole was first described in 1889 by C. Hart Merriam, a renowned mammalogist, during his tenure as chief of the Biological Survey in Washington, D.C. Specimens were obtained from the type locality near Kamloops, British Columbia, northwest of Montana. The scientific notation applied by Merriam is still in use today. The generic distinction, *Phenacomys,* is derived from the Greek combination, phenakos, meaning an "imposter," and mys, meaning "mouse;" Merriam's generic notation refers to this species' close resemblance to the montane vole, *Microtus montanus,* with which it is sympatric. The specific epithet, *intermedius,* is from the Latin combination inter which means "between," and medius which means "middle," again likely a reference to this species' intermediate appearance between a vole and a mouse.

Description: The heather vole is grayish-brown above and whitish-gray below, with a short, sharply bicolored tail that is less than one-half its body length. Its feet are pale gray to white, with the hind feet well-haired over the posterior half of the sole and has 6 pads. Distinct dental characteristics can also be used for identification (Foresman 2001). As its generic name implies, the heather vole is quite similar to the montane vole and easily can be misidentified as such. Dental characteristics are the most reliable means of properly distinguishing between these 2 species (Foresman 2001). Care must be taken as well to distinguish this species from the northern bog lemming as general appearances are similar. Here, accurate measurements of tail length and dental characteristics will identify the heather vole. Lighter color, tail length, or dental characteristics can also be used to separate the heather vole from the meadow vole and long-tailed vole (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 143.1(10)/♀ 136.3(10); Ta = ♂ 33.8(10)/♀ 32.7(10); HF = ♂ 16.8(10)/♀ 17.4(10); E = ♂ 15.3(6)/♀ 14.6(8); M [g(*n*)] = ♂ 27.5(10)/♀ 25.2(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The heather vole is predominantly a boreal species widely distributed across the Canadian provinces from the northern half of the Yukon and Northwest Territories, throughout Quebec and



Map 49. Distribution of the heather vole, *Phenacomys intermedius.*

most of Newfoundland. Its range is disjunct, extending as far southwestward as central California, Nevada, and northern New Mexico. Southwestern populations are associated with higher elevation habitats of the montane taiga biome.

Ecology and Behavior: A denizen of coniferous forests, the heather vole prefers dry, open areas particularly where a heath understory exists. It is also widely associated with the shrubby edge between forested stands and open areas, and moist, mossy meadows. In Montana, the heather vole occurs in subalpine spruce fir forests where dense ground canopy is present. Here it is associated with shrubs such as mountain heath and dwarf huckleberry. It extends above timberline to the krummholz and moist meadows of the alpine tundra and may be found in lower elevation, ponderosa pine–Douglas fir forests where an understory of twinflower and bearberry is present.

The heather vole is strictly herbivorous, feeding during the evening and night on an assortment of foliage. During summer the most common plant consumed is bearberry. Beargrass, bush willow, and dwarf birch foliage and fruits are also used. In autumn and spring, seeds and lichens are consumed, while bark is heavily utilized during winter months. The hypgeous fungus *Endogone* has also been reported in the diet. The heather vole is fond of caching food near the entrance to its burrows both during winter and summer.

The burrow of the heather vole is short and shallow, being no more than a few centimeters underground, with a connecting tunnel only 1 m in length between holes. Entrances are often overgrown making detection difficult. Nests are found directly under rocks, logs, or discarded wooden planks. Nests themselves are formed from moss, leaves, and grass and are 10 cm in diameter. Chambers within 0.5 m of the nests are designated latrine sites.

Several reports of high populations are possible, although the general consensus is that the heather vole is trap shy and rarely seen. It is likely much more abundant throughout its more northern distribution than in the more isolated pockets to the south.

Reproduction: In Alberta breeding extends from May to August, although this period may be shortened at higher elevations. Females may breed several times during this period (seasonal polyestry) producing 2–3 litters. Following a gestation of 19–24 days, 3–5 young ($\bar{x}$ = 3.62–3.8 for young-of-the-year, 4.41–5.9 for adults, with a range of 2–8) are born. Weaning begins on day 14 and is completed no later than day 19. Females reach sexual maturity in 4–6 weeks and may breed the summer of their birth; males do not reach sexual maturity until the following spring.

Status: Widely dispersed and uncommon.

McAllister, J. A., and R. S. Hoffmann. 1988. *Phenacomys intermedius.* Mammalian Species 305:1–8.

Bushy-tailed Woodrat
Neotoma cinerea

Bushy-tailed woodrat (*Neotoma cinerea*). See plate 5.

Scientific Name: The bushy-tailed woodrat was first described by George Ord, early naturalist and co-founder of the Academy of Natural Sciences of Philadelphia, in 1815. His description was based on a specimen caught by Captain Meriwether Lewis on 2 July 1805, while Lewis and Clark's expedition was portaging around the Great Falls of the Missouri River, in present day Great Falls, Montana (Cascade County). Originally identified as *Mus cinereus,* the current usage, *Neotoma cinerea,* was applied by Spencer Fullerton Baird, in 1858. The generic designation, *Neotoma,* is from the Greek combination, Neo, which means "new," and tomos, which means "cut;" a reference to a new species with "cutting teeth," in other words a rodent distinct from the previously known group *Mus.* The specific epithet, *cinerea,* is from the Latin, cinis, meaning "grayish or ashen," a reference to its pelage color.

Description: The original field notes of Meriwether Lewis describing the bushy-tailed woodrat are as useful today, in identifying important physical characteristics, as they were in 1805. Lewis wrote that this species was:

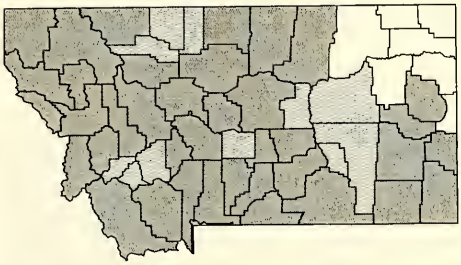
> "... somewhat larger than the common European rat (Norway rat), of lighter colour; the body and outer part of the legs and head of a light lead colour, the belly and inner side of the legs white as were also the feet and years (ears). the toes were longer and the ears much larger than the common rat; the ears uncovered with hair. the eyes were black and prominent the whiskers very long and full. the tail was reather longer than the body and covered with fine fur or poil (hair) of the same length and colour of the back. the fur was very silkey close and short." (Moulton 1987b:352; parenthetic statements by this author)

Both Lewis and William Clark kept field notes; Clark's entry for this day described the animal's tail as, "... long & hairey like a ground Squirrel...." (Moulton 1987b: 354). The bushy-tailed woodrat should not be confused easily with any other rodent species in the state. The large, rounded, naked ears; protruding black eyes; distinctly white feet; and long, bushy tail (from which its vernacular name is derived) clearly distinguish the bushy-tailed woodrat, and make it 1 of the prettiest species in the state.

Measurements: [mm(*n*)]: TL = ♂ 338.6(10)/♀ 381.3(10); Ta = ♂ 160.5(10)/♀ 159.2(10); HF = ♂ 41.3(10)/♀ 44.5(10); E = ♂ 28.0(7)/♀ 32.3(4); M [g(*n*)] = ♂ 294.3(10)/♀ 315.1(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The bushy-tailed woodrat extends throughout western North America, from the Yukon and Northwest Territories through British Columbia and Alberta, to California, Arizona, and New Mexico. Eastward extensions project into the Dakotas and Nebraska.

Ecology and Behavior: The bushy-tailed woodrat can be found in a variety of



Map 50. Distribution of the bushy-tailed woodrat, *Neotoma cinerea*.

habitats from the dry, semi-desert environment of southeastern Montana, to the higher elevation, forested regions of the west. It prefers to build nests in vertical crevices of rock outcroppings along streams or draws, on cliff faces, and in boulder fields up to, and above, timberline. Caves are also used, as are abandoned out-buildings. Nests are hidden within often elaborate structures built of sticks, dried vegetation, bone fragments, fur, and whatever other debris might be handy. These complex dens are enlarged, over many generations, until they may reach several meters in diameter and height. Bottle caps, tinfoil, pieces of glass, and other bright objects are sequestered in these structures. Their collection of these trinkets has resulted in the garnering of another vernacular name, that of "pack rat." The nest proper is cup-shaped or globular, consisting of shredded bark, dried grasses, moss, leaves, and fabric fibers accumulated on excursions. Den sites often include multiple nests.

The bushy-tailed woodrat is nocturnal and active throughout the year. It is primarily herbivorous feeding on a notably wide assortment of vegetation. Leaves of forbs and woody plants, and conifer needles, are highly preferred, although fruits, seeds, and fungi are also eaten. Fecal analyses from bushy-tailed woodrats in southcentral Idaho found that pricklypear, Munro gloemallow, and vetches made up more than 70% of the plant fragments identified (Johnson and Hansen 1979). Occasionally insects will also be consumed. In autumn, woodrats spend considerable time cutting and drying large quantities of foliage which is later stored in crevices for use during winter.

Woodrats feed, urinate, and defecate on ledges which serve as perches and resting places. Because they often remain at 1 locality for generations, these latrines which they share, frequently accumulate material over an extended period of time. These sites are immediately recognizable by the dark brown, crystallized urine which forms into a mass, often coating the rocks or cave walls near the den site. Latrines and the debris surrounding dens sites, which are sometimes formed over hundreds of years, are referred to as "middens." These have been shown to provide a wealth of paleontological evidence. Plant materials, such as pollen and leaves, insect parts, and animal bones, which become trapped in the urine, are often preserved for thousands of years as the urine crystallizes (Phillips and van Devender 1974). These middens have served not only as the source of paleovegetation data for the western United States, but have also provided significant insight into the woodrat's historic foraging behavior.

Reproduction: Reproductive data here was obtained from a laboratory colony established from a wild population on the Utah–Nevada border. The breeding season extends from late January, or early February, through late July, with litters born into August. Peak litter production occurs between March and June. Females are polyestrous and exhibit a post-partum estrus. Gestation lasts between 27 and 32 days, and average litter size is 3.5 (range 1–6). Litter sizes above 4 may suffer losses as the female can only nurse 4 young at one time. Although captive females can produce up to 7 litters/year, the number successfully produced in the wild is surely less.

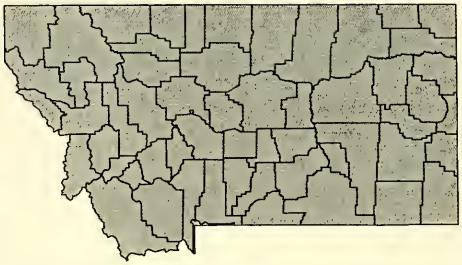
Young are weaned between days 26 and 30; sexual maturity is not commonly reached until the year following birth.

Status: Common.

Smith, F. A. 1997. *Neotoma cinerea*. Mammalian Species 564:1–8.

Muskrat
Ondatra zibethicus

Muskrat (*Ondatra zibethicus*).



Map 51. Distribution of the muskrat, *Ondatra zibethicus*.

Scientific Name: First described by Carolus Linnaeus in 1758 from specimens obtained in eastern Canada. Originally designated as *Castor moschatus,* this nomenclature was changed to the present usage by the early 1800s. The generic designation, *Ondatra,* is from the North American Iroquois Indian word, ondatra, for "muskrat." The specific epithet, *zibethicus,* is from the Latin zibethicus, which means "musty-odored."

Description: The largest microtine in North America and the 3rd largest rodent in Montana (the beaver and porcupine are larger), muskrats have many distinct, physical characteristics which relate to its semi-aquatic existence. Hind feet are partially webbed and possess stiff hairs along the toes, modifications for swimming. Tail is long, scaly, and laterally flattened, providing an effective rudder while in the water and an effective heat exchanger for thermoregulation. It has a compact body with a short head; small, rounded ears; and a valvular mouth with lips that close behind the incisors, similar to pocket gophers. This last feature allows the animal to feed while underwater. The fur, which is most often dark brown in color (although many lighter variants exist), is quite buoyant and nearly waterproof due to the dense underfur. Longer guard hairs are less numerous and more coarse. Perineal musk glands, the products of which are responsible for the vernacular name, are well-developed and used to scent trails and den sites, during the breeding season. The only species with which the muskrat might be confused, and this only from a distance, is the beaver. The distinctive appearance of its hind feet and tail distinguish it from all other Montana mammals.

Measurements: [mm(*n*)]: TL = ♂ 542.9(10)/♀ 459.5(4); Ta = ♂ 23.7(9)/♀ 221.8(4); HF = ♂ 74.8(10)/♀ 74.8(4); E = ♂ 15.8(6)/♀ 20.7(3); M [g(*n*)] = ♂ 913.6(10)/♀ 962.5(10). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The muskrat extends from Alaska across all of the Canadian provinces southward, covering most of the United States, with populations reaching northern Mexico.

Ecology and Behavior: The muskrat, like the beaver, inhabits all riparian habitats, from small creeks and streams to larger river systems. It is particularly fond of ponds and marshes, where its distinctive houses can be free-standing or built into mud banks. These houses, formed above ground from available vegetation, typically cattail

and bulrush, are of 2 common types. The most familiar is the "dwelling lodge," much the same in appearance as the beaver lodge, although considerably smaller in size. In winter, these lodges are 1–2.5 m in length, 0.9–2.5 m in width, and 0.4–1 m high, with walls averaging 48 cm in thickness; summer lodges are 12–30% smaller, with walls half as thick. These lodges have 1 central chamber (although up to 3 may be formed in the winter and up to 7 in the summer), and are entered from below waterline by 1 or more tunnels. A 2nd type of house, termed the "pushup," is typically constructed by pushing submerged, aquatic vegetation such as pondweed up into ice cracks, forming a dome above the ice. These pushups, and more elaborate "feeder" lodges, are built around, and radiate from, the main dwelling lodge during winter (Stevens 1953). These foraging lodges are positioned at distances from the main dwelling lodge that approximate the optimal distance which the muskrat can swim under the ice pack (MacArthur 1992). These "way stations" allow the animals to forage over a relatively large area during the winter, in relative safety from predation, with only short, periodic forays into cold water.

Besides lodges and feeding stations, the muskrat is well-known for constructing canals around its homerange which connect the more permanent structures and provide ready access to deeper water. These activities often conflict with human interests; dikes of farm ponds, and other impoundments, may be breached with subsequent drainage. Considerable effort and expenditures have gone toward the management and control of this species.

Muskrats are small and can chill easily in winter when they swim in cold water to feed. A great deal of energy must be expended to accomplish these forays, at great metabolic cost (MacArthur 1984). These physiological debits are partially offset by behavioral activities. The well-insulated, dwelling lodges and placement of feeder lodges, are 2 such factors. Communal relationships established during winter, and associated huddling behavior also help animals after they forage (Bazin and MacArthur 1992; MacArthur 1984). As many as 6 individuals may aggregate in 1 nest, for as long as 15 hours/day (MacArthur 1980). This behavior accomplishes 2 things. It readily allows each animal's body heat to be shared and reduces their individual surface areas exposed to the wet, thereby reducing heat loss. Possibly more important, the heat that is generated quickly warms the nest chamber, thereby providing the animals with a warm microenvironment. Energetic costs are reduced accordingly (Fig. 52).

Muskrats are primarily herbivorous, feeding both in late afternoon and late evening on the more common aquatic plants available at any given location. Roots and stems of cattails and bulrush are highly used, although many other plants such as sedges and arrowheads will suffice. A large variety of animal foods are also eaten by muskrats. These include frogs, fish, fresh-water clams, snails, and crayfish.

A single, annual molt occurs during the summer, with maximal regrowth by late autumn, and provides muskrats with an extremely dense, lustrous, winter pelt. A large volume of air can be trapped in this fur (calculated at an amazing 21.5% of the average total dry volume of the fur) providing great buoyancy and insulation. Such high quality fur has, of course, not escaped the attention of the commercial trapper. In Montana alone, 11,727 animals were harvested in 1995. This number, although, was down considerably from the 40,000+ individuals trapped in 1987, when market prices were higher.

Reproduction: In more northern latitudes such as Montana, breeding begins in the spring and extends into the summer. In southeastern Idaho peak production of 1st litters occurs in May, with litters produced throughout August. An average of 2 litters (rarely 3) are produced/season, with 7 (2–10) young/litter. Gestation extends for 25–

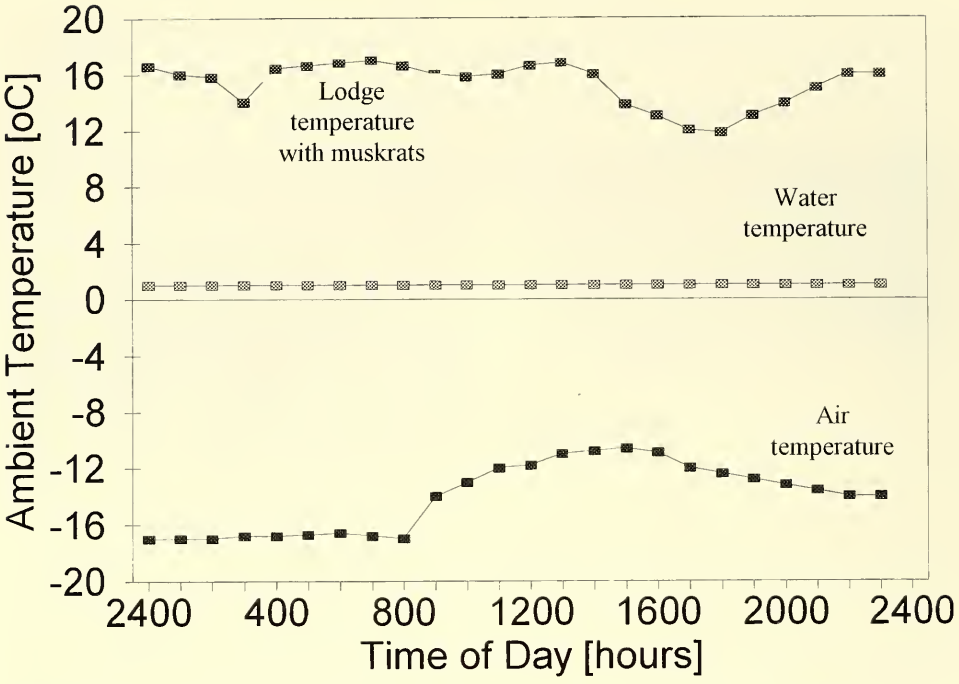


Fig. 52. Microenvironment of the muskrat lodge during the winter illustrating its insulative properties (MacArthur and Aleksiuk 1979).

30 days, and females exhibit a post-partum estrus.

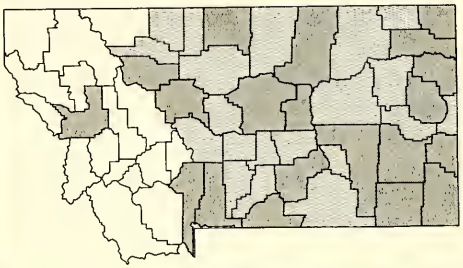
Young, weaned at 4 weeks, reach adult size by 6 months, but do not reach sexual maturity until the spring after their birth.

Status: Common.

Willner, G. R., G. A. Feldhamer, E. E. Zucker, and J. A. Chapman. 1980. *Ondatra zibethicus*. Mammalian Species 141:1–8.

Northern Grasshopper Mouse
Onychomys leucogaster

Northern grasshopper mouse (*Onychomys leucogaster*). See plate 5.



Map 52. Distribution of the northern grasshopper Mouse, *Onychomys leucogaster.*

Scientific Name: The northern grasshopper mouse was first described in 1841 by Maximilian Prinz zu Wied from specimens obtained near Fort Clark in Oliver County, North Dakota. His designation, *Hypudaeus leucogaster,* was changed to the present usage, *Onychomys leucogaster,* by Spencer Fullerton Baird in 1858. The generic designation, *Onychomys,* is from the Greek onychos, meaning "claw," and mys, meaning "mouse;" a reference to the long, curved claws which the northern grasshopper mouse uses to grasp prey. The specific epithet, *leucogaster,* is derived from the Greek combination, leukos, which means "white," and gaster, which means "belly."

Description: One of the most distinctive characteristics of the northern grasshopper mouse is its short, thick tail (measuring less than half of its body length), which ends bluntly. In overall body form, the northern grasshopper mouse is stocky, with relatively large forefeet; soles of both forefeet and hind feet are furred. The body is distinctly bicolored, with dorsal pelage varying from light brown, to grayish or buffy, and white ventral pelage. Skull and dental characteristics are diagnostic (Foresman 2001). The northern grasshopper mouse, at 1st glance, might be confused with the 2 species of *Peromyscus* present in Montana. However, it can be clearly distinguished by its distinctly shorter tail, large forefeet, and unique morphology of the lower jaw (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 132.0(3)/♀ 147.0(5); Ta = ♂ 37.7(3)/♀ 38.0(5); HF = ♂ 19.7(3)/♀ 19.8(5); E = ♂ 16.2(3)/♀ 15.6(5); M [g(*n*)] = ♂ 29.1(4)/♀ 38.0(6). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The northern grasshopper mouse extends from Alberta, Saskatchewan, and Manitoba to northeastern Mexico, and from the central regions of Washington and Oregon and the northeastern portions of California to the central United States.

Ecology and Behavior: The northern grasshopper mouse inhabits open, sagebrush deserts and grassland areas, although it is associated with more mesic regions within these. Male–female pairs construct nest burrows in sandy substrate. These bur-

rows are typically 15 cm under the surface, 51 cm long, with 2 entrances, and a centrally located nest chamber. One or both entrances may be plugged during the day. These other burrows are built within an individual's home range as well: the retreat burrow, the cache burrow, and a miscellaneous category which included those used for defecation. Retreat burrows, as the name implies, are used in an emergency to hide. These are nothing more than hollowed-out cavities in the sand, about the same size as nest burrows, but without the enlarged nest chamber. Cache burrows are constructed for storage of seeds with entrances which are covered with sand. Shallow, 5 cm depressions are formed within which the animal defecates. Other depressions may be formed as the animal sand-bathes during self-grooming activities. Secretions exuded from anal glands are left in these latter depressions which serve to mark territories.

Active year-round, the northern grasshopper mouse is strongly nocturnal in its activity patterns. Its vernacular name refers to its primarily carnivorous diet, feeding on grasshoppers (order Orthoptera), beetles (Coleoptera), moths (Lepidoptera), and other insects. The northern grasshopper mouse is aggressive and can kill, and eat small vertebrates. The deer mouse, montane vole, and Great Basin pocket mouse, among other mammals, are prey for this predator, as are small birds and reptiles. Plant materials, particularly seeds, are also consumed during winter, when prey are less available. Seeds are stored in large quantities as a hedge against severe weather and the paucity of arthropods.

The northern grasshopper mouse is particularly vocal, with a repertoire of at least 4 categories of sounds. These vocalizations are most often used for communication between individuals.

Territorial behavior is well-developed in this species. Besides marking its territory with anal gland scent, the grasshopper mouse is among the most aggressive of small mammals. It can attack and kill animals as large as the cotton rat, fully 3 times its size, when its warnings go unheeded.

Reproduction: In Utah, breeding in the wild extends from February through August. In captivity, 3 to 6 litters may be produced in a season; productivity in the wild is highly dependent on prevailing weather conditions and food availability. One to 6 young (mean usually 3–4) are born after a gestation of 26–37 days. When litters are conceived during a post-partum estrus, gestation lengths may be slightly extended. Laboratory-raised individuals, both males and females, become sexually mature as early as 4 months of age. In the wild breeding probably does not occur until the breeding season following the year of their birth.

Status: Common although not abundant.

McCarty, R. 1978. *Onychomys leucogaster.* Mammalian Species 87:1–6.

White-footed Mouse
Peromyscus leucopus

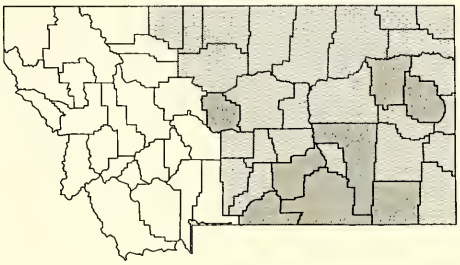
Scientific Name: The white-footed mouse was first described in 1818 by Constantine Samuel Rafinesque, a somewhat eccentric naturalist, from specimens he collected in Kentucky. He denoted this species as *Musculus leucopus.* The current name was first employed by O. Thomas in 1895. The generic designation, *Peromyscus,* is apparently from the Greek combination pero, which means "defective," and myskos, which means "mouse." The exact reasoning behind this appellation is unknown. The specific epithet, *leucopus,* also of Greek origin, is derived from the combination leu-

kos, which means "white," and pous, which means "foot."

Description: The white-footed mouse is quite similar to the other member of this genus in Montana, the deer mouse. Both species are bicolored. The white-footed mouse is dark brown to gray above, with a white ventral surface. Dorsal pelage of individuals in Montana is more grayish than that of the deer mouse. One of the best external characteristics to distinguish these species is the degree to which the tail appears bicolored. In the white-footed mouse, although the tail is dark above and light below, this demarcation is not nearly as sharp as in the deer mouse. Also the tip of the tail of the white-footed mouse lacks a tuft of white hairs, as is present in the deer mouse. The distribution of these species may also be helpful in identifying specimens. With the exception of the deer mouse, the white-footed mouse should not be confused with other murid rodents in Montana. The sharply bicolored nature of the body pelage, with contrasting brown–gray, dorsal versus white, ventral color, and clear "mouse" versus "vole" appearance, identifies this species as a *Peromyscus.* Often it is difficult to distinguish between the white-footed mouse and deer mouse in the field.

Measurements: [mm(*n*)]: TL = ♂ 167.0(2)/♀ 170.4(5); Ta = ♂ 74.5(2)/♀ 75.6(5); HF = ♂ 21.0(2)/♀ 20.3(5); E = ♂ 17.5(1)/♀ 15.5(2); M [g(*n*)] = ♂ 24.3(2)/♀ 25.7(5). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The white-footed mouse extends across the eastern two-thirds of the United States, reaching its western limits along a line which runs from just inside Canada, in the Canadian provinces of Alberta and Saskatchewan, southward through Montana, Wyoming, Colorado, and New Mexico, and jutting into Arizona. Southward extensions occur into central and eastern Mexico. In Montana, specimens have been obtained only from central and southeastern Montana, although earlier range maps (Hoffmann et al. 1969) suggested a distribution across the eastern half of the state, connecting with a known population at Milk River, Alberta, just north of Toole County.



Map 53. Distribution of the white-footed mouse, *Peromyscus leucopus.*

Ecology and Behavior: Habitats most frequently occupied by the white-footed mouse include those with structural complexity and canopy cover. Brushy ravines and old fields with considerable woody debris are preferred. Riparian areas may also be used and coniferous forests with the requisite understory structure. More open grass prairies are avoided.

Nest sites are chosen in a wide variety of microhabitats from logs, tree stumps, and rock outcrops, to unoccupied burrows of other species. Interestingly, this species is highly arboreal often building nest structures above ground. Nests are constructed from available materials including leaves, grass, moss, shredded bark, hair, and feathers. Exhibiting a nocturnal foraging pattern, the white-footed mouse is omnivorous in its dietary preferences. Insects make up the largest proportion of food selected, however seeds, and to a lesser degree green vegetation, are also consumed. Seasonal shifts reflecting availability of these items are well documented. White-footed mice hoard food (Sanchez and Reichman 1987), a behavior which can be coupled with its ability to undergo daily torpor, to offset thermal extremes.

The exhibition of torpor in the white-footed mouse is highly variable among in-

dividuals within a population and between populations (Pierce and Vogt 1993). Cold temperatures are the primary trigger for this behavior; food deprivation further stimulates torpor bouts, especially in individuals less genetically predisposed to respond. Unlike true hibernation, these bouts of lowered body temperature are short in duration, (lasting an average of 4 hours) and core temperatures reached are not as low (body temperatures range from 17.3–28°C—Pratt 1983).

Unlike microtine rodents, the white-footed mouse does not exhibit wildly fluctuating population levels. Behavioral patterns, which include dominance, habitat partitioning based on sex, and pheromonal affects on reproductive development, interact to regulate population densities. Average life span in the wild is relatively short as is true for other small rodents.

Reproduction: A gestation of 22–23 days occurs in non- lactating individuals. If impregnation occurs in females who are simultaneously lactating, gestation may be lengthened to 36–37 days. Average litter sizes range from 3.0–5.4. Latitude, temporal factors, age, and body size, contribute to this variation. Large litter sizes and seasonal breeding activity, centered around spring and late summer, are probable in Montana.

Adult body size is approached by 6 weeks, and sexual maturity follows soon thereafter.

Status: Locally abundant.

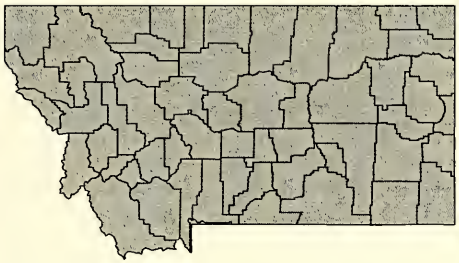
Lackey, J. A., D. G. Huckaby, and B. G. Ormiston. 1985. *Peromyscus leucopus.* Mammalian Species 247: 1–10.

Deer Mouse
Peromyscus maniculatus

Deer mouse (*Peromyscus maniculatus*). See plate 6.

Scientific Name: The deer mouse was first described by Wagner in 1845 from specimens collected in Labrador and originally identified as *Hesperomys maniculatus* (Hall 1981:679). The current name was applied by Bangs in 1898 (Hall 1981:679). The generic designation, *Peromyscus*, is from the Greek combination, pero, which means "defective," and myskos, which means "mouse." The exact reasoning underlying this appellation is unknown. The specific epithet, *maniculatus*, is Latin for "small handed."

Description: One of the most distinctive mice in the state, the deer mouse can be readily identified by its sharply bicolored appearance. Its dorsal pelage is predominantly grayish-brown, darker along the midline, and blending to a lighter brown laterally. Ventral pelage and limbs are white, this color continues to the underside of the tail, thus a sharp demarcation is apparent. Ears are relatively large and scantily haired, eyes are large and black. Only 1 species in the state may be confused easily with the deer mouse; this is the closely related white-footed mouse. Often the white-footed mouse is more grayish in appearance (although juvenile deer mice have gray pelage), and their tail is slightly longer. The demarcation between dark and light color



Map 54. Distribution of the deer mouse, *Peromyscus maniculatus.*

on the tail is also less distinct in the white-footed mouse. Also, in Montana, the white-footed mouse is only found in the eastern and some central regions, thus distribution may be useful in making a determination. Often it is difficult to distinguish these 2 species in the field.

Measurements: [mm(*n*)]: TL = ♂ 163.0(10)/♀ 160.3(10); Ta = ♂ 19.3(10)/♀ 19.9(10); HF = ♂ 68.0(10)/♀ 68.5(10); E = ♂ 17.2(5)/♀ 17.8(6); M [g(*n*)] = ♂ 22.7(10)/♀ 22.5(10). Dental formula: i 1/1, c 0/0, p 0/0, 3/3, total 16.

Distribution: The deer mouse is widely distributed across the United States, Canada, and Mexico. Except in the southeastern United States, the deer mouse is 1 of the most common mammals in North America.

Ecology and Behavior: Deer mice occur in a wide variety of habitats throughout the state, from sagebrush deserts and dry grasslands in the east, to montane and subalpine forests of the west, and the alpine tundra of the southwest–southcentral region. In forested areas it is more common where drier conditions exist and in more open canopied stands which have a fair amount of ground structure. Such habitat preferences may separate the deer mouse from the white-footed mouse. The latter species prefers riparian zones, where more moist conditions exist and avoids the more open grasslands inhabited by the deer mouse.

Deer mice may construct burrows, but more often use those made by other small mammals. Nest sites are found under logs, rocks, at the base of stumps, and under lumber or other debris, near human habitations. Deer mice often also construct arboreal nests (Wolff and Durr 1986; Wolff and Hurlbutt 1982). Nests are cup-shaped, formed from shredded grasses or other plant material and fur.

Deer mice are strictly nocturnal as might be suspected from their large eyes. They forage throughout night on a wide variety of plant and animal materials, as befits their omnivorous diet. Seeds are a mainstay of the diet, particularly during winter. Green vegetation is consumed during spring and summer, although a high percentage of the diet at this time consists of insects (grasshoppers, beetles, caterpillars). Other food items include fungi, berries, and nuts of many plants. Although active throughout the year, the deer mouse is capable of short bouts of torpor as with the white-footed mouse. However, unlike many rodent species in which torpor is an obligate behavioral response to environmental extremes (e.g., ground squirrels and chipmunks), only certain individuals in a population of *Peromyscus* actually are capable of entering this physiological state (Pierce and Vogt 1993). Populations from harsher climates have a higher percentage of such individuals, demonstrating natural selection in response to such environmental conditions. The frequency of torpor increases during the coldest winter months, while the molt to a winter pelage occurs earlier in autumn. These behavioral, physiological, and anatomical responses to local environmental changes are coupled with increased nest building activity and food hoarding (primarily seeds—Pierce and Vogt 1993). The latter behavior will offset short periods of food shortage during extremes in temperature. In areas of heavy snow, the deer mouse moves about under this insulating layer. One other behavioral mechanism employed by the deer mouse to offset cold temperatures is communal nesting. Several deer mice will huddle together within a nest to share body heat

(Millar and Derrickson 1992). Interestingly, deer mice may actually huddle with white-footed mice, a somewhat unusual behavior (Wolff and Hurlbutt 1982).

Extreme population fluctuations, noted for many microtine species, are not observed in deer mice. Variation in numbers between 1 year and the next may occur due to environmental changes however, and population sizes notably increase in autumn as young born during summer months mature.

Reproduction: Breeding extends from early spring to late autumn (March to October) in Montana. Gestation lasts for 23 days; mean litter sizes vary from 3.0–5.0 (McCabe and Blanchard 1950). Females exhibit a post-partum estrus, thus 3–4 litters may be produced during a single season. Young are weaned at 3.5 weeks as the next litter is being born. Both males and females reach sexual maturity at 1–2 months (Clark 1938) and, if born early in the season, are capable of breeding their 1st summer. Such a breeding strategy allows for a large burst in autumn populations; however, mortality on deer mice is high, and individuals rarely live past 1 year, thus significant population shifts are not often seen.

Status: Common.

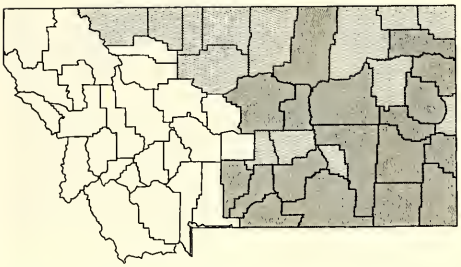
Western Harvest Mouse
Reithrodontomys megalotis

Scientific Name: The western harvest mouse was first described in 1858 by Spencer Fullerton Baird, founder of the United States National Museum. Specimens were obtained from the type locality between Janos, Chihuahua, and San Luis Spring, Grant County, New Mexico. The scientific name *Reithrodontomys megalotis,* applied by Baird, is still accepted today. The generic distinction, *Reithrodontomys,* is from the Greek combination, reithron, meaning "channel or groove," odontos, referring to "tooth," and myos, which means "mouse;" thus "groove-toothed mouse." The specific epithet, *megalotis,* is also of Greek origin, from the combination megas, which means "greatest or large," and otos, meaning "ear"; thus "large eared."

Description: The western harvest mouse presents a grizzled appearance, with grayish to blackish guard hairs dorsally, underlain by underfur which is banded with a buffy strip tipped in black. Venter is white. As the scientific name indicates, the western harvest mouse has large ears and distinct grooves on the front surface of its upper incisors (Foresman 2001). The sharply bicolored tail is long (>body length), sparsely haired, and scaly. In general appearance, the western harvest mouse most closely resembles the deer mouse because of its large ears and bicoloration. Overall, the combination of grizzled body color, large ears, and scaly, sparsely-haired tail will clearly identify this species. Only 1 other rodent in Montana possesses grooved incisors, and this species (northern bog lemming) has very different habitat preferences.

Measurements: [mm(*n*)]: TL = ♂ 136.5(10)/♀ 139.9(5); Ta = ♂ 63(10)/♀ 64.3(5); HF = ♂ 17.0(10)/♀ 16.8(5); E = ♂ 13.7(10)/♀ 13.1(4); M [g(*n*)] = ♂ 12.3(10)/♀ 12.0(4). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The western harvest mouse is widely distributed throughout western North America, extending from southern British Columbia, Alberta, and Saskatchewan to southern Mexico. Populations span east to west, from Indiana and Illinois to the California coast. Interestingly it is absent from the Rocky Mountain chain which runs across Montana, Wyoming, and Colorado.



Map 55. Distribution of the western harvest mouse, *Reithrodontomys megalotis.*

Ecology and Behavior: The western harvest mouse occurs in a wide variety of habitats, from tall native grasses to overgrown pastures and weedy fencerows. It also frequents brushy riparian habitats, and drier (although not xeric) sagebrush shrublands.

Nests are globular in shape and constructed on or slightly above ground (up to 1 m), within dense vegetation. Shredded plant materials form the outer walls, while softer "down" plant materials, such as thistle and milkweed, line the inner chamber. One or more openings enter the nest from the base.

Seeds are the preferred diet (thus this species is termed "granivorous") although arthropods are heavily used during spring and early summer.

Foraging activity is confined to the night, with increased movements during rainy or overcast periods. Avoidance of bright, moonlit nights is surly a behavioral response to predation pressures. In many regions the western harvest mouse may remain active throughout the year. Hibernation may occur in some populations and western harvest mice readily enter torpor when exposed to low temperatures (4.8°C) for extended periods of time (14.5 hr) or to water stress.

Reproduction: Although the western harvest mouse can breed throughout the year in more southern regions, in Montana breeding is seasonal, beginning in the spring and continuing into early autumn. Gestation lasts 23–24 days with an average litter size of 3.64. Females are polyestrous and have a post-partum estrus, thus can produce many litters throughout the breeding season. Weaning is completed by 3 weeks and females may reach sexual maturity as early as 4 months.

Status: Common although not abundant.

Webster, W. D., and J. K. Jones, Jr. 1982. *Reithrodontomys megalotis.* Mammalian Species 167:1–5.

House Mouse
Mus musculus

House mouse (*Mus musculus*). See plate 6.

Scientific Name: The house mouse was first described by Carolus Linnaeus from specimens obtained in Upsala, Sweden (1758). Linnaeus developed the binomial system of nomenclature which we use today. The scientific designation applied by Linnaeus, *Mus musculus,* is still retained today. Two subspecies, *M. m. brevirostris* and *M. m. domesticus,* were introduced into North America, the former from the Iberian peninsula into the southern United States by Spanish trading vessels, and the latter

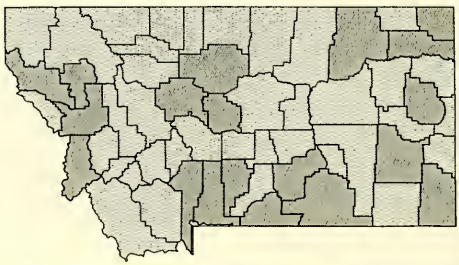
from England, France, and Germany into Alaska (Schwarz and Schwarz 1943). The generic designation, *Mus,* is Latin for "mouse;" the specific epithet, *musculus,* is Latin for "small mouse."

Description: The house mouse engenders the characteristics commonly associated with what is popularly known as a "mouse." Black eyes protrude from a grayish-brown dorsal pelage. The venter is a lighter brown to gray or even whitish. Tail is naked with scaly rings; ears are large and only lightly haired. With careful observation, the house mouse should not be confused with any other rodent in Montana. The distinctly mouse-like appearance will separate this species from voles. The most distinguishable characteristic is the scaly nearly naked tail, the appearance of which is found only in the house mouse and the introduced Norway rat. Other Montana mice, such as the white-footed mouse, deer mouse, and western harvest mouse, all possess more strongly contrasting dorsal–ventral body pelage and haired tails.

Measurements: [mm(*n*)]: TL = ♂ 162.9(10)/♀ 161.8(5); Ta = ♂ 74.5(10)/♀ 79.7(5); HF = ♂ 18.3(10)/♀ 18.5(5); E = ♂ 13.3(6)/♀ 14.0(1); M [g(*n*)] = ♂ 22.7(10)/♀ 22.9(6). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The house mouse is widely distributed throughout the world. Originally native to 3 regions of central and eastern Asia (Turkestan and Iran, southern Russia, and Japan), house mice first dispersed throughout Europe, Africa, and Latin America in association with human migrations, before becoming established in North America in the early 16th century (Schwarz and Schwarz 1943). The house mouse is closely associated with human habitations and the cultivation practices of man.

Ecology and Behavior: The house mouse is capable of adapting to a variety of habitats, primarily those near humans. Old fields, and those under cultivation, are preferred during the warmer months; as winter approaches these animals will migrate into outbuildings, granaries, and inhabited homes (Evans 1949). Although quite secretive, their presence is often confirmed by fecal droppings that are left in cupboards and closets.



Map 56. Distribution of the house mouse, *Mus musculus.*

Nests are constructed of materials at hand. Grass, and other dried vegetation, may be used to form globular nests, as may paper, cloth, feathers, or other soft items. Nests are often hidden outside under logs and piles of lumber or debris. Nests may also be built within buildings, in garages, the walls of a home, and even in cupboards and stored boxes. The house mouse is quite social, forming colonies consisting of 1 adult male, several females, and their resultant offspring (Bronson 1979).

One reason for the great success of the house mouse is its omnivorous diet. Cultivated crops are often eaten both in the field and in storage bins. In addition seeds, roots, fungi, or other plant materials, and many insects and even meat will be consumed. House mice will also eat paper products, such as books and other household items.

Animal densities may be maintained at relatively stable levels in commensal populations (10/m^2 are often realized), but field populations may undergo extreme fluctuations in numbers (Bronson 1979). An outbreak in Kern County, California reached levels exceeding 205,000/ha; and for over 4 months nearly 4 billion mice were thought

to infest an area 18 miles in diameter (Hall 1927)!

Active throughout the year, and primarily nocturnal, the house mouse will venture out during daylight hours in secluded areas such as barns and garages. They can easily squeeze through openings smaller than 1.25 cm, thus they can enter buildings almost at will.

The house mouse is considered, along with the Norway rat, to be 1 of the most destructive rodents in the world. Significant economic losses occur each year through their consumption of harvested grains and the spoilage which occurs as a result of their feces and urine. Their role as a vector for many diseases (discussed below) also causes hardship although, interestingly, this is the same species which has been raised in the laboratory for research purposes for more than half a century. The "white" lab mouse has been instrumental as an animal model for medical research and has been used extensively in the development of medicines for the treatment of human diseases.

As a cautionary note, the house mouse hosts numerous parasites (fleas, ticks, mites, lice) and is capable of transmitting a variety of bacterial and viral diseases. Diseases such as bubonic plague, Hanta virus, tularemia, leptospirosis, and rickettsial pox are hosted by wild members of this species. Routine cleaning of brush and piles of debris around homes, which would otherwise provide nest sites, will prevent them from becoming established within residences. It is often a good idea to place mouse traps near entrance ways, such as garage doors, in autumn because these animals attempt to move indoors.

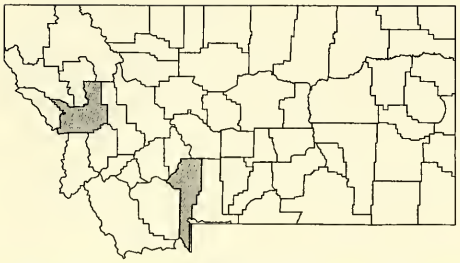
Reproduction: The gestation period is similar to that of other small rodent species, 19–21 days. With a post-partum estrus, and a breeding season which extends for 8–9 months, from early spring to late autumn (Brown 1953), the house mouse can be highly prolific. Females are reproductively active throughout the year cycling at 4–6 day intervals. In captivity, up to 14 litters may be produced in a year; in the wild, particularly in more northern areas such as Montana, 4–6 litters are more common. Litter sizes range from 2–13, commonly 5–7. Young are weaned by 3 weeks, with sexual maturity attained by 6 weeks.

Status: Common.

Norway Rat
Rattus norvegicus

Scientific Name: The Norway rat was first described by Berkenhout in 1769 from specimens collected in Norway (Hall 1981: 839). Initially identified as *Mus norvegicus,* the present notation was not used until 1916 (Hall 1981:839). The generic designation, *Rattus,* is Latin for "rat." The specific epithet, *norvegicus,* is a Latinized word to denote the country of origin of the type specimen.

Description: The Norway rat is a large bodied, stocky rodent with large, naked ears and a scaly, round tail. Dorsal pelage is coarse and grizzled, grayish-brown in color interspersed with black. Ventral color is a consistent gray. Dental characteristics clearly identify this species (Foresman 2001). The Norway rat should not be confused with any other small mammal in the state. Its size, and obvious naked, scaly tail clearly distinguish it from all other species. Although the muskrat also has a scaly tail, it is flattened, and its larger overall body size, markedly different pelage characteristics, and aquatic lifestyle easily separate the 2 species. The bushy-tailed woodrat, although somewhat similar in overall size, is also



Map 57. Distribution of the Norway rat, *Rattus norvegicus.*

clearly distinguished by its body characteristics: large, busy tail, very large ears, and dense, soft pelage.

Measurements: [mm(*n*)]: TL = ♂/♀ 316–460; Ta = ♂/♀ 122–215; HF = ♂/♀ 30–45; E = ♂/♀ no measurements; M [g(*n*)] = ♂/♀ 195–485. Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: Found throughout North America except the colder northern regions of Canada.

Ecology and Behavior: The Norway rat was an introduced species to the North American continent, by British ships from Europe during the late 1700s when the Revolutionary War was being fought. From this introduction, it quickly spread throughout the eastern region and continued its march westward. Later, in the mid 1850s, the Norway rat was inadvertently introduced along the Pacific coast as ships offloaded miners during the gold rush era. Montana was the last state in which Norway rats became successfully established (Tryon 1947b). Initial invasions were controlled, but between 1920 and 1925 the Norway rat became forever established in the state, 1st in Lewistown (Cates 1937). Secondary invasions from North Dakota in 1936 allowed this species to spread across the eastern-most portion of the state by 1947 (Tryon 1947b). Currently Norway rats can be found in most of Montana's larger cities and are a common inhabitant of many rural properties.

The Norway rat is extremely adept at living in close association with humans and is thus thought of as a commensal species. It is comfortable around water and is a strong swimmer and climber; skills that have allowed it to swim to docked ships and climb up moorings for travel around the world. It is found in town and city dumps and potentially anywhere garbage and trash accumulates. Norway rats are also found in, and around, grain elevators and outbuildings, particularly where animal feed is stored.

Nests, constructed from leaves and twigs, are found under debris around houses and outbuildings. Norway rats can dig extensive tunnels. Its omnivorous diet has allowed it to adapt and survive a wide range of conditions. Most notably recognized and vilified for eating grains, other plant materials are readily used, as are a wide array of animal species. Invertebrates, fish, birds, and small mammals are eaten, as is carrion. Many instances exist where Norway rats have even killed newborn piglets and lambs and attacks on humans have been reported (Nowak 1991).

Although primarily nocturnal, Norway rats may venture out during daylight hours. Where 1 animal exists, many will be found, as it is a colonial species with a highly structured social hierarchy. Twelve or more individuals may make up a colony, sharing food sources and nest sites. These resources are effectively defended against individuals from other colonies by outward aggression.

The Norway rat is often thought of as the worst animal pest of humans. Significant economic losses due to crop damage or grain storage occur yearly. In its effort to gain access to food sources, to water, or salt, it chews on pipes, electrical wiring, or anything else in its way. Losses to such activity are estimated in the hundreds of millions of dollars a year in the United States alone.

Known to be a reservoir and carrier for numerable serious diseases affecting humans, among which is Bubonic plague (*Yersinia pestis*), considerable efforts have been expended to control this species.

Reproduction: One of the most prolific of mammals, the Norway rat can breed

year-round in Montana. Females are polyestrous and exhibit a post-partum estrus. With a gestation period of 21 days they could theoretically produce 12 or more litters/year. More commonly 3–6 litters are produced with an average litter size of 8–9 (range of 3–22). Newborn Norway rats grow rapidly and are weaned by 3 weeks. Sexual maturity is reached when individuals are 3 months old.

Status: Locally common although not abundant.

Northern Bog Lemming
Synaptomys borealis

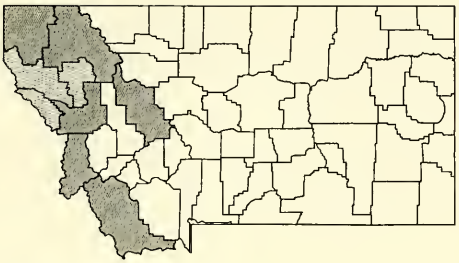
Northern bog lemming (*Synaptomys borealis*). See plate 6.

Scientific Name: The northern bog lemming was first described by John Richardson (1828), an English naturalist, from specimens obtained at Fort Franklin, Mackenzie, Northwest Territories, the type locality. Originally designated *Arvicola borealis,* the current name was applied in 1907 (Osgood 1907). The generic distinction, *Synaptomys,* is from the Greek combination synapto, which means "to unite," and mys, which means "mouse;" a reference to the "link" which this species appears to provide, based on its intermediate physical characteristics, between the true lemmings and meadow mice. The specific epithet, *borealis,* is from the Latin meaning "northern."

Description: The northern bog lemming has a grizzled coat, reddish-brown on the dorsum grading into a gray venter. Ears extend noticeably beyond the body fur and are sparsely haired on their edge. Its tail is extremely short, only equal to or slightly longer than the hind foot and is bicolored. One characteristic shared with the true lemmings is its relatively long, loose coat. Dental characteristics are also unique (Foresman 2001). In hand, the northern bog lemming could be confused with the heather vole or the meadow vole, with which it is sympatric. It can be separated from both species by careful measurement of the tail, this being shorter in the bog lemming. Pelage color in the meadow vole is a darker brown and should be the 1st distinguishing characteristic considered. Grooved upper incisors and shape of upper and lower molariform teeth are the most diagnostic dental characteristics for the bog lemming (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 120.0(10)/♀ 120.0(6); Ta = ♂ 22.6(10)/♀ 21.3(6); HF = ♂ 18.6(10)/♀ 18.1(6); E = ♂ 13.6(10)/♀ 12.5(3); M [g(*n*)] = ♂ 25.1(10)/♀ 22.7(5). Dental formula: i 1/1, c 0/0, p 0/0, m 3/3, total 16.

Distribution: The northern bog lemming is widely distributed across northern North America from Alaska across the Canadian provinces to the Atlantic coast. Eastern populations extend southward through Maine and into New Hampshire. Other southward extensions occur in Minnesota and along the northern borders of Washington, Idaho, and Montana.



Map 58. Distribution of the northern bog lemming, *Synaptomys borealis*.

Ecology and Behavior: As its vernacular name implies, the northern bog lemming is primarily associated with bogs and fens, consistent with its boreal distribution. Such habitats are characterized by extensive sphagnum moss mats. Willow, dwarf birch, and sedges are additional vegetative components common to sites where bog lemmings have been collected. Forested overstories from lodgepole pine with Engleman spruce interspersed, to larch, and subalpine fir surround the sphagnum bogs.

Records of individuals captured in other habitat types (dry alpine–subalpine ridge, lodge pine–western larch, old-growth western hemlock) may reflect dispersing individuals, as high quality habitat occurs near most of these sites.

Although widely distributed across Canada, the northern bog lemming is considered uncommon to rare throughout its range; this is surely the case for the northern bog lemming in Montana. Until 1991, when this author and his graduate student began an intensive study of the bogs in western Montana, only 6 specimens had been collected in the state. Primarily as a result of our study, and more recently the extensive efforts of Reichel and Beckstrom (1994), 20 individuals have now been captured.

The northern bog lemming is active throughout the year and apparently throughout the day and night. Nests, constructed from grasses and sedges, are hidden in short underground burrows or under logs and stumps, in sphagnum mounds or grass tussocks. Runways may be constructed through the vegetation, although the northern bog lemming will readily use runways of other microtines.

Although the diet is mostly herbaceous, with green vegetation being consumed; snails, slugs, and other invertebrates are frequently taken. Fresh feces have a distinctly green appearance unlike that of other voles. This characteristic may be used to identify this species' presence although the color quickly disappears as the feces age.

Normal yearly population fluctuations, which reflect the spring–summer breeding cycle and winter die-off, occur, with population densities from 6–35 individuals/ha (Banfield 1974).

The northern bog lemming may be a relic species whose present distribution, particularly in Montana, reflects the glacial history of this region. Forced to migrate southward as the Pinedale Glacial advance occurred (18,000–10,000 years before present), the northern bog lemming, through its habitat preferences, established itself in the boreal climate of the time. As the glacial mass receded northward over the past 10,000 years small northern bog lemming populations remained behind, ultimately becoming trapped in islands of boreal (bog) habitat as broader habitat changes occurred.

Reproduction: In Canada, breeding begins in May and extends into August. After a gestation of 23 days, 1–8 young are born ($\bar{x} = 4$). Weaning occurs between days 16 and 21, with sexual maturity attained by 5–6 weeks. Adult females are polyestrous and have a post-partum estrus (Banfield 1974).

Status: Rare.

Family Sciuridae—Squirrels*

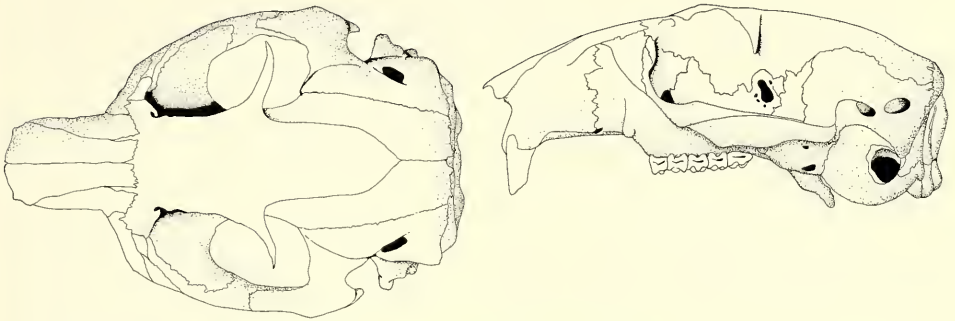


Fig. 53. Skull of a squirrel (*Spermophilus*).

White-tailed Prairie Dog
Cynomys leucurus

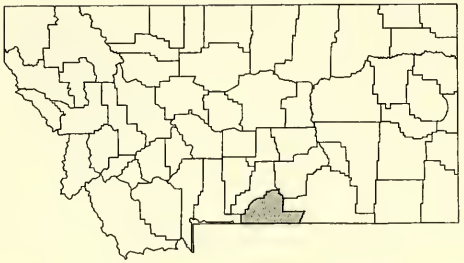
Scientific Name: The white-tailed prairie dog was first described by C. Hart Merriam, chief of the United States Biological Survey from 1885–1910, in 1890 from specimens obtained from Fort Bridger, Uinta County, Wyoming. The genus *Cynomys* was first proposed 75 years earlier, in 1817, by Constantine Sameul Rafinesque, a somewhat eccentric naturalist who followed his own rules of nomenclature. Rafinesque based his description on specimens collected by Charles Le Range, a member of the Lewis and Clark Expedition. The generic designation, *Cynomys,* is derived from the Greek combination kynos, which means "dog," and mys, which means "mouse." The specific epithet, *leucurus,* is from the Greek leukos, which means "white," and oura, which means tail, thus "white-tailed."

Description: The white-tailed prairie dog is the smaller of 2 species of *Cynomys* found in Montana. The dorsal pelage, which is yellowish-buff mixed with black, blends into a ventral color of lighter pinkish-buff. Distinct brownish-black patches occur above the eyes and on the cheeks. As its vernacular name implies, its tail is tipped in white. General body conformation is stout with a very short, flattened tail. Further modifications for semi-fossorial existence are short legs and well-developed claws, particularly on the forefeet. Distinct skull and dental characteristics can be used to further distinguish between the 2 species (Foresman 2001). Stout body and short tail are characteristics that separate this species from ground squirrels in the genus *Spermophilus.* The white-tipped tail and structure of the skull (Foresman 2001) will clearly distinguish this species from the other member of the genus *Cynomys,* the black-tailed prairie dog.

Measurements: [mm(*n*)]: TL = ♂ 357.4(2)/♀ 308.5(2); Ta = ♂ 58.5(2)/♀ 45.0(2); HF = ♂ 60.5(2)/♀ 52.5(2); E = ♂ 12.0(2)/♀ 11.0(1); M [g(*n*)] = ♂ none/♀ 494.0(2). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The white-tailed prairie dog is confined to the intermontane plains

* For representative skull characteristics of this taxonomic family refer to Fig. 53.



Map 59. Distribution of the white-tailed prairie dog, *Cynomys leucurus*.

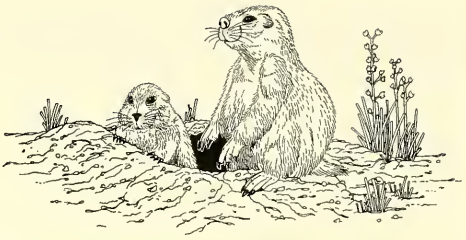


Fig. 54. Prairie dog sitting on guard for the colony.

of Montana, Wyoming, Utah, and Colorado, with the core of its distribution in Wyoming. The most northern extension of its range enters southcentral Montana, and in the Bighorn Basin of Carbon County (Hoffmann et al. 1969). As of 1977, 15 colonies had been identified in Montana, covering a total area of 285 ha (Flath 1979).

Ecology and Behavior: The white-tailed prairie dog is a denizen of xeric mixed stands of shrubs and grasses. Colonies in Montana are associated with 1 of 2 habitat types, those dominated by Nuttall saltbush with lesser amounts of big sagebrush (Flath 1979) and those in which poverty sumpweed and winter fat ("white sage") predominate. Blue grama and prairie junegrass, among other grasses and forbs, characterize 1 site. The habitats in which Montana populations are found (1,148–1,768 m) are somewhat unusual, as throughout its range this species is an inhabitant of high montane basins.

Although not a social species (unlike the black-tailed prairie dog), this prairie dog does establish large colonies, together defined as "towns," with densities of prairie dogs ranging from 0.7 to 8.4/ha. Burrows, constructed without the cooperation of other members of the colony, typically have multiple entrances. These may have either a significant accumulation of earth formed into a mound at the opening or no excavated soil at all. Burrows with litters (identified as "maternity" burrows) are easily recognized by the greater accumulation of earth on the mound itself and by accessory digging within the mound. Accessory excavations are probably the work of new pups who are learning the craft.

Emerging from hibernation in late February to early March, white-tailed prairie dogs remain active during daylight hours until entering hibernation again, most often in late July or early August. Juveniles often wait until late autumn before entering hibernation, presumably because they are unable to attain adequate fat stores until this time. Heterothermic abilities are similar to those of other hibernating rodents (Bakko and Nahorniak 1986).

Activity patterns are influenced by daily temperature. During spring and late summer days, when ambient temperatures are more consistently mild, animals are most active during the afternoon. Animals forage around burrow entrances or sit upright, carefully surveying their surroundings for signs of an intruder (Fig. 54). Sharp, high-pitched, alarm calls, somewhat similar to a dog's bark and from which the vernacular name "dog" is derived, are emitted if an intruder is sighted. As daytime temperatures rise during the summer, a bimodal pattern of activity is adopted, with foraging confined to early morning and late afternoon. Foraging radiates out from the burrow entrance, distances covered determined by existing weather conditions. Adult home ranges are slightly smaller than those of juveniles (5.9 versus 6.9 ha), who are often distributed on the periphery of the colony.

Contrary to general perceptions, this herbivore prefers annual forbs rather than range grasses. Food studies on Colorado populations showed that early spring diets

rely heavily on sagebrush and saltbush, with a shift towards green forbs (dandelion and species of goosefoot), as these become locally available. Animals take advantage of western wheatgrass as it goes to seed in the summer, shifting to the flowers of rabbitbrush in the autumn. Although highly vilified as a competitor with livestock for high quality forage grasses, the white-tailed prairie dog does not generally cause deterioration of range conditions and may actually enhance range recovery after overgrazing has occurred. Their foraging activities, and behavior of cutting vegetation around their burrows for a more unobstructed view, may still, however, lead to range destruction during stressful periods of severe drought combined with livestock overgrazing. In many parts of its range, much effort and expense is still allocated to control this species; such widespread extermination efforts have led to a reduction of its historic range and recent consideration for federal listing as an endangered species.

Although predation may play a role in the population dynamics of a colony, as white-tailed prairie dogs are an easy target for badgers, black-footed ferrets, coyotes, foxes, and golden eagles, 1 of the most significant controlling mechanisms is the prevalence and destructiveness of sylvatic plague (*Yersinia pestis*). This same disease was responsible for the epidemic which swept Europe in the Middle Ages (Menkens and Anderson 1991). Responses to such an epizootic event in the white-tailed prairie dog vary considerably within, and between, colonies, although significant die-offs (up to 85% of the colony) are common. Transmittal of sylvatic plague into the human population by infected fleas is possible, and care must be taken when working with, or around, infected prairie dog colonies. Several cases of plague in humans have been reported in Montana and Wyoming in recent years, although these were probably not derived from prairie dogs.

Interest in the white-tailed prairie dog has increased significantly over the past 15 years, when it became obvious that the black-footed ferret (federally listed as an endangered species) relies heavily on this species (and the black-tailed prairie dog) for food (Campbell et al. 1987). Rather than perpetuating extensive extermination programs developed over the past 100 years, federal management guidelines designed to enhance prairie dog populations and maintain the prairie dog ecosystem, have now been developed.

Reproduction: In Wyoming, the breeding season begins rapidly, on emergence from hibernation, in March to early April. Males emerge 2–3 weeks before females with renewed testicular development already well underway. Peak testicular development is attained within 2 weeks following emergence, coincident with the appearance of females and resultant copulation. Testicular regression, signaling the end of the breeding season, begins soon thereafter (Bakko and Brown 1967).

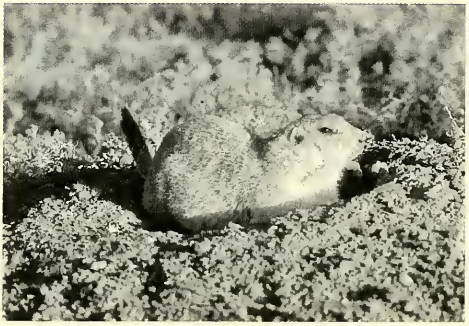
Females also begin reproductive recrudescence prior to emergence from hibernation, exhibiting mature follicles at this time. Copulation occurs within days of female emergence and, after a 27–33 day gestation, a single litter is produced in late April to early May. Litter sizes, based on embryo counts or uterine swellings, averaged 5.64.

Reproductive development in juveniles begins by late summer to early autumn, although sexual maturity is not reached until 1 year of age.

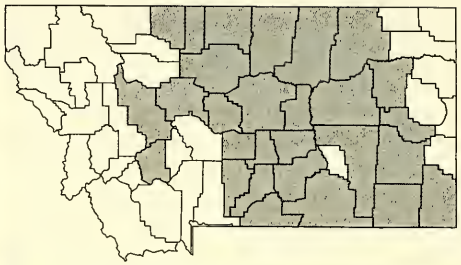
Status: Restricted to Carbon County and not abundant.

Clark, T. W., R. S. Hoffmann, and C. F. Nadler. 1971. *Cynomys leucurus*. Mammalian Species 7:1–4.

Black-tailed Prairie Dog
Cynomys ludoviscianus



Black-tailed prairie dog (*Cynomys ludoviscianus*). See plate 6.



Map 60. Distribution of the black-tailed prairie dog, *Cynomys ludoviscianus*.

Scientific Name: The black-tailed prairie dog was first described by George Ord in 1815 based on observations by Meriwether Lewis and William Clark during their expedition to the Pacific Coast and on specimens sent by them to then President Thomas Jefferson. Ord, a naturalist and co-founder of the Academy of Natural Sciences of Philadelphia in 1812, named this new species *Arctomys ludoviscianus*. Spencer Fullerton Baird, founder of the United States Biological Survey, was 1st to apply the current taxonomic distinction, *Cynomys ludoviscianus*, in 1858. The generic designation *Cynomys* is from the Greek combination kynos, which means "dog," and mys, which means "mouse;" a reference to Lewis' 1806 description of this species as having a bark, ". . . being much that of the little toy dogs . . ." (Moulton 1993:76). The specific epithet, *ludoviscianus*, is a Latinized form of Ludwig (Louis). Ord applied this scientific appellation to the "Louisiana marmot," the common name given to this species, in recognition of Lewis and Clark's expedition to the Louisiana Territory.

Description: The black-tailed prairie dog is a stout, short-legged animal with a short, flattened tail, and well-developed claws particularly on the forefeet. Ears are short and rounded, extending only as far as the dorsal pelage. Color above is pinkish-cinnamon, with black-buff tipping; ventral surface is whitish to buffy-white. Tail is tipped in black hairs, from which the vernacular name is derived. The stout body conformation and short tail can be used to distinguish this species from ground squirrels of the genus *Spermophilus*, as can the convergent nature of the upper toothrow (Foresman 2001). The black-tipping on the tail, and skull differences (Foresman 2001), clearly separate this species from the similar white-tailed prairie dog.

Measurements: [mm(*n*)]: TL = ♂ 397.3(9)/♀ 391.5(6); Ta = ♂ 88.9(9)/♀ 79.4(5); HF = ♂ 62.7(9)/♀ 57.7(6); E = ♂ 12.0(1)/♀ 13.0(2); M [g(*n*)] = ♂ 940.5(8)/♀ 1,061.5(3). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The black-tailed prairie dog is widely distributed across the central portion of North America from southwestern Saskatchewan to northern Mexico. It ranges across 11 states from Montana and the Dakotas to Arizona, New Mexico, and Texas, with its easternmost extension on the eastern border of Nebraska.

Ecology and Behavior: William Clark, of Lewis and Clark fame, described

their 1st encounter with the black-tailed prairie dog, at the foot of the Tower in Boyd County, Nebraska as follows:

> September 7th, 1804:
> "... discovered a Village of Small animals that burrow in the grown (those animals are Called by the french Pitite Chien) Killed one & Cought one a live by poreing a great quantity of water in his hole we attempted to dig to the beds of one of thos animals, after diging 6 feet, found by running a pole down that we were not half way to his Lodges.... the Village of those animals Covs. about 4 acrs of Ground on a Gradual decent of a hill and Contains great numbers of holes on the top of which those little animals Set erect make a Whistleing noise and whin allarmed Slip into their hole —" (Clark, 1804 as cited in Moulton 1987a: 53).

This species was new to science at the time; Clark, recognizing this fact, sent a live animal back to President Thomas Jefferson the following spring. He collected several other specimens which were sent to the Peale Museum in Philadelphia, from which Ord published the 1st scientific description. Amazingly, the 1st specimen collected at this time, of a species new to science, was, "... cooked for the Capts dinner ...," as indicated by Sergeant Ordway, a member of the expedition (Cutright 1969:79). These explorers did not agree on a common name; Lewis apparently preferred "barking squirrel," whereas Clark referred to it as either the "ground rat," or the "burrowing squirrel" (Cutright 1969:80). Ordway probably suggested the name "pairie dog," which is now used.

The black-tailed prairie dog inhabits grasslands and sagebrush semi-desert areas throughout the Great Basin. In general it occupies lower elevation plains while the white-tailed prairie dog uses higher elevation mountain basins. Extensive aggregations ("colonies" grouped into even larger "towns") are formed as these individuals construct their burrow systems in the open grasslands. Burrows typically have a cone-shaped mound of earth 0.33–1 m high at their entrance which provides a barrier to flooding and a perch from which to view the surroundings. Tunnels extend vertically down from the entrance for 1–3 m at which point they continue horizontally for an additional 3–5 m. A nest chamber, excavated off a side tunnel, is lined with dry grass. Burrow densities, measured recently in a prairie dog town in Phillips County, ranged from 13.5–246.4 burrows/ha (Reading et al. 1989).

During efforts to locate suitable sites in Montana for the reintroduction of black-footed ferrets, over 700 active prairie dog colonies were located including colonies of white-tailed prairie dog (Campbell 1989). In total these colonies extend over 40,469 ha, with a majority of populations (77%) concentrated in Blaine, Carter, Custer, Garfield, Phillips, Prairie, and Valley counties.

Black-tailed prairie dogs are strict herbivores feeding on a variety of plant materials in their environment. Western wheatgrass, six weeks fescue, Russian thistle, pricklypear, and saltbush are the predominant components consumed (Kelso 1939). Availability and abundance of plant species obviously influences foraging decisions, although green vegetation, particularly perennial grasses and forbs, are preferred. As green vegetation becomes limited in the autumn a shift is made to roots, although green winter vegetation such as fourwing saltbush and plains pricklypear are still relished.

The feeding preferences of this species have been a topic of interest and research for over 100 hundred years, as human activities have come more and more into direct conflict with existing prairie dog populations. Initially, as settlements progressed westward and cultivated crops were developed, black-tailed prairie dogs took advantage of this ready food source, much to the aggravation of homesteaders. With the introduction of cattle onto the range and their subsequent overgrazing and depletion of native tallgrass stands, such as western wheatgrass, short grasses spread. These vegetative disturbances

actually favored the black-tailed prairie dog, and their towns increased in size. Since they were able to survive on severely damaged range, people assumed that prairie dogs were actually responsible for these changes, and considerable extermination efforts began. These efforts were so successful that large areas formerly occupied by the black-tailed prairie dog are now devoid them. Although extermination efforts are still in force today, the black-tailed prairie dog is recognized as being beneficial to maintenance of healthy range conditions and for their ability to offset damage created by cattle overgrazing. This is not to say, however, that they may not contribute to habitat destruction during drought or when land is severely overgrazed by cattle.

The black-tailed prairie dog is far more social than the white-tailed prairie dog. Members of a colony (2–35 individuals) group socially into "coteries": assemblages of an adult male, several adult females, yearlings of both sexes, and young-of-the-year. Several coteries, in turn, are loosely grouped into "wards" covering 2–4 ha in size and defined by vegetative barriers. Many wards form a "town," the extent of which may exceed 100 ha. Present day "dog towns," however, can in no way match those seen previously. Historical records describe 1 town in western Texas that spanned 64,000 km^2 and was estimated to have 400,000,000 animals! The coterie functions as the social foundation of a town. Members freely interact with one another and may participate in burrow construction and defense of their territory against members of an adjacent coterie. Dispersal of both males and females between coteries (intracolony dispersal) occurs, presumably to provide greater access to mates and to reduce competition for food.

Foraging takes up much of an individual's daily activity. During summer, movements are confined to early mornings and late afternoons; inclement weather will force these animals to remain within the protection of their burrows. Animals forage at increasingly greater distances from their burrows as the number of individuals above ground increases. Apparently a greater number of individuals, on the lookout for predators, provides more security to those individuals foraging.

Unlike the white-tailed prairie dog and a majority of the closely related ground squirrels in the genus *Spermophilus,* the black-tailed prairie dog does not routinely hibernate. They may enter a state of dormancy if exposed to colder temperatures and deprived of food, however, they can not rewarm if temperatures stay low. Winter activity is highly variable. Many individuals may remain below ground and live off stored fat (no vegetation is cached), whereas others routinely come above ground in the middle of winter to feed.

Sylvatic plague (*Yersinia pestis*) occurs in Montana populations of black-tailed prairie dogs. Epizootics can spread throughout a prairie dog town with devastating effects; die-offs of 85% (white-tailed prairie dog) and 100% (Gunnison's prairie dog) have been recorded. Care should be taken when working in and around colonies to avoid contact with these animals, and their fleas, which are the normal vector for the transmittal of this disease to humans.

Reproduction: The breeding season extends from mid-March to early April with most litters born in early May following a 28–33 day gestation. Most conceptions occur within a 1 week period of time. A single litter of 1–13 young ($\bar{x}$ = 4.6–5.0) is produced, the young remaining within the burrow for the first 5 weeks. Emergence above ground and initial foraging activities occur by week 6, with weaning completed shortly thereafter. Juveniles do not reach adult body size until their 2nd summer (1 year of age), and many females and all males do not attain sexual maturity until their 2nd year. Attainment of sexual maturity appears to be directly influenced by colony size and habitat availability.

Status: Locally abundant.

Hoogland, J. L. 1996. *Cynomys ludovicianus.* Mammalian Species 535:1–10.

Hoary Marmot
Marmota caligata

Hoary marmot (*Marmota caligata*). See plate 7.

Scientific Name: The hoary marmot was first described by Johann Friedrich Eschscholtz in 1829 from specimens collected near Bristol Bay, Alaska (Hall 1981: 374). Eschscholtz was a professor at the University at Dorpat, who sailed around the world as a naturalist collecting and describing plant and animal specimens. *Arctomys caligatus,* the name applied at this time, was changed to *Marmota caligata* by Joel Asaph Allen (1903). The generic designation, *Marmota,* is Latin for "marmot." The specific epithet, *caligata,* is from the Latin, caligatus, which means "booted." This is a reference to the hoary marmot's feet, which are black.

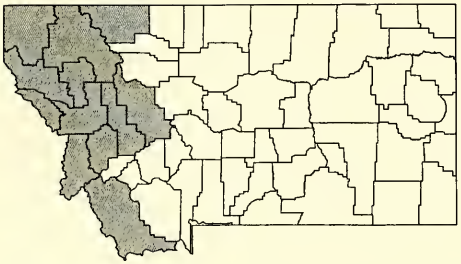
Description: The hoary marmot is a large, stocky rodent with a short neck; broad, rounded head; and small, well-furred ears. Its feet have strong claws and a pad on the sole of the hind foot that is subcircular in appearance (a diagnostic characteristic). Tail is long, nearly one-third of body length. Body pelage is coarse, with a high concentration of guard hairs tipped in white. This tipping imparts a grizzled appearance on the animal, hence the vernacular name "hoary." The head and anterior one-third of the body are most often black with white-tipped hairs; feet are black and the belly is a lighter wash. The hoary marmot is 1 of 2 species of marmot in the state, the other being the yellow-bellied marmot. Color differences are often distinct enough to separate the species. Differences in the shape of pads on soles of the hind feet are also diagnostic. In Montana, where these species are sympatric, the hoary marmot occupies alpine habitats, while the yellow-bellied marmot will be in lower elevations.

Measurements: [mm(*n*)]: TL = ♂ 734.1(10)/♀ 686.6(10); Ta = ♂ 211.9(10)/♀ 208.6(10); HF = ♂ 92.9(10)/♀ 90.2(10); E = ♂ 27.3(3)/♀ 32.3(3); M [kg(*n*)] = ♂ 5.4(10)/♀ 4.3(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The hoary marmot ranges from the northernmost reaches of Alaska through the Yukon and the western edge of the Northwest Territories into British Columbia. Here its distribution diverges, 1 extension proceeding southeastward into western Alberta, Montana, and Idaho, and the other into Washington. In Montana, populations are known from the Purcell Mountains, Whitefish and Lewis ranges, North and South Bitterroot, Mission, Rattlesnake, Flink Creek, Anaconda-Pintlar, and Beaverhead mountains, although this species only can be considered common in Glacier National Park (Hoffmann et al. 1969).

Ecology and Behavior: Hoary marmots are tightly tied to alpine and subalpine slopes, especially throughout western Montana. Sedges, a variety of grasses, and several forbs (including lupine, doorweed, and glacier lily) identify their habitat. In Glacier Park, where hoary marmots are abundant, their habitat is characterized by krummholz forested areas near talus slopes.

As with the yellow-bellied marmot, the hoary marmot prefers rock outcroppings



Map 61. Distribution of the hoary marmot, *Marmota caligata.*

and large boulder fields for its burrows. Colonies of hoary marmots construct many burrows throughout a rock slope. The marmots rely on the natural interstices between boulders to provide entrance ways into their tunnel system. Most nest burrows have >1 opening. Olympic marmots line their nests with dried sedges and grasses, and hoary marmots probably do so as well, as they collect and carry dried grasses into their burrow systems. Boulder fields in which hoary marmot populations exist lie adjacent to grassy, alpine meadows, providing animals ready access to food.

The hoary marmot is a vegetarian with a distinctly selective palate. Although many plant species occur in abundance in their alpine meadows, these marmots are somewhat choosey in what they eat. In Montana, many flowering species are eaten, notably silky lupine, indian paintbrush, and the glacier lily. Grasses and sedges are also consumed, and meat may be taken when plants are scarce.

The hoary marmot spends most of its life hibernating, routinely 8–8.5 months a year, in Montana, from September to early May. During this period, their metabolic rate decreases, and their body temperature decreases to near ambient conditions existing within the insulated nest chamber. On emergence in the spring, individuals accumulate weight rapidly and continue to do so throughout the summer so that by early autumn individuals may nearly double their weight. The weight gained in any given summer depends on the time of snow melt that spring, in other words how early new vegetation becomes available.

By late summer hoary marmots become less and less active in preparation for entrance into hibernation. The "trigger" for this significant metabolic shift into an extended torpor is a combination of food deprivation and colder temperatures, in association with the animal's own body condition (i.e., increased fat storage). Hoary marmots aggregate during this period and can reduce individual metabolic costs, by sharing body heat and reducing their overall surface area for heat dissipation.

Hoary marmots have activity cycles during the summer that are similar to those of the yellow-bellied marmot. Foraging begins just after sunrise and continues through mid-morning. Feeding bouts are interspersed with sunning activity, with the latter accounting for a high percentage (>44%) of the time spent above ground during clear days. During cloudy days, less time is spent sunning and more is spent foraging. Activity resumes during late afternoon as well, with animals entering their dens as evening approaches. During early spring and late summer, diel activity becomes unimodal, with the peak around midday. These patterns reflect the need to avoid overheating and hypothermia.

The social structure of hoary marmots is somewhat stronger than that exhibited by yellow-bellied marmots. A typical colony consists of 1 adult male, 1 or more adult females, 2-year olds, yearlings, and young-of-the-year. Yearlings remain with the mother during their 1st year, dispersing as 2-year olds. Adult females breed every other year, thus they do not have to contend with young and yearlings simultaneously. Often more than 1 colony may be contiguous, with members of each interacting daily.

Reproduction: Reproductive activity begins immediately on emergence from hibernation in late spring. Gestation lasts 30 days. Average litter size of 3-year olds is smaller ($\bar{x}$ = 2.3) than older individuals ($\bar{x}$ = 4.2). Young are weaned between late July

and early August; those individuals weaned earlier will enter hibernation in a heavier condition, and subsequently have a better chance of surviving the winter. Both males and females are sexually mature as 3-year olds; breeding occurs biannually.

Status: Common, particularly in Glacier National Park.

Barash, D. P. 1989. Marmots: social behavior and ecology. Stanford University Press, Stanford, California.
Frase, B. A., and R. S. Hoffmann. 1980. *Marmota flaviventris.* Mammalian Species 135:1–8.

Yellow-bellied Marmot
Marmota flaviventris

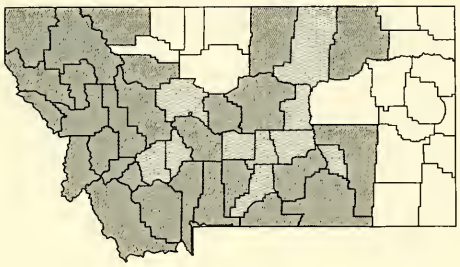
Yellow-bellied marmot (*Marmota flaviventris*). See plate 7.

Scientific Name: The yellow-bellied marmot was first described by James J. Audubon, the famous ornithologist and naturalist, and John Bachman, a close friend, in 1841 from specimens obtained at Mount Hood, Oregon. Originally given the scientific name *Arctomys flaviventer* by these individuals, the currently accepted name, *Marmota flaviventris,* was proposed by Howell in 1915. The generic designation, *Marmota,* is Latin for "marmot." The specific epithet, *flaviventris,* is from the Latin combination, flavus, which means "yellow," and ventris, which means "belly," thus "yellow-bellied."

Description: The yellow-bellied marmot is a large, robust rodent with a broad head; small, well-furred ears; and a tail nearly one-third of body length. Its color is yellow-brown to tawny above, with a distinctly yellow venter (from which its vernacular name is derived). In Montana, many color variants are seen; animals may be darker brown above, and their ventral surface may be darker as well, approaching a more orangish appearance. Buffy to yellowish neck patches may be seen. Many dorsal guard hairs have dark shafts with lighter tipping giving this animal's coat a "frosted" look. The feet possess strong claws and an oval pad exists on the posterior portion of the sole of the hind foot. The other marmot in Montana, the hoary marmot, is larger than the yellow-bellied marmot. Color differences are great enough to preclude most confusion; the hoary marmot in overall appearance is whitish-gray and is distinctly "grizzled." Hind sole pads in the hoary marmot are also subcircular rather than oval.

Measurements: [mm(n)]: TL = ♂ 552.3(10)/♀ 553.1(10); Ta = ♂ 165.7(10)/♀ 160.1(10); HF = ♂ 77.3(10)/♀ 75.2(10); E = ♂ 27.3(4)/♀ 27.0(3); M [kg(n)] = ♂ 2.8(10)/♀ 2.3(10). Dental formula: i 1/1, c 0/0, p 2/1, 3/3, total 22.

Distribution: The yellow-bellied marmot extends from southcentral British Columbia and southern Alberta to southern California and across to South Dakota, Colorado, and New Mexico. In Montana, the



Map 62. Distribution of the yellow-bellied marmot, *Marmota flaviventris*.

yellow-bellied marmot is found as far east as Valley and Rosebud counties (Hoffmann et al. 1969). They are noticeably absent along a core area which extends from Glacier Park southeastward to encompass the Mission, Swan, Flathead, and Lewis mountain ranges.

Ecology and Behavior: The yellow-bellied marmot prefers rocky outcroppings and talus slopes within which to build its nests. Although most burrow sites exist in such natural settings, populations have been found near Missoula within the rock fill for a highway and the concrete fill deposited along a stream bank. Burrows are constructed 1 m under ground and 3–4 m back from their entrance, with a nest cavity at the terminus. More than 1 entrance may be present and some branching of the tunnel system may occur. Importantly, these nest sites must not only provide protection for the individual and any offspring that are born, but must serve as hibernacula during winter months. Appropriate sites for hibernacula may be a limiting factor for the yellow-bellied marmot, ultimately determining its overall distribution.

Throughout much of its range in Montana the yellow-bellied marmot is most often associated with lower elevation habitats, as compared to the hoary marmot which exists in alpine settings. As you progress southward, however, out of the range of the hoary marmot, the yellow-bellied marmot is found in all suitable, alpine habitats. This observation led Hoffmann (1974) to suggest that their absence, where sympatric with the hoary marmot, is due to competitive exclusion. The yellow-bellied marmot is seen on the Beartooth Plateau, in westcentral Montana, at elevations above 3,350 m.

The yellow-bellied marmot is colonial, often living in groups (termed "harems") consisting of an adult male, several adult females, and their resultant offspring. Other individuals may live alone or in a pair, depending on availability of habitat and each individual's behavioral makeup.

Since the yellow-bellied marmot is herbivorous, burrow sites are chosen adjacent to areas which provide adequate vegetation. Animals show a distinctly bimodal pattern of activity during spring and summer emerging just after sunrise to begin foraging. Feeding continues throughout morning hours interspersed with quiet periods spent sunning. A similar pattern is followed in the afternoon. Although preference is shown for particular plant species while foraging, a wide variety of flowers and forbs are eaten, as are grasses. When flowering plants go to seed in late summer, these may be eaten in abundance. The ingestion of seeds at this time may be a behavioral response in preparation for hibernation; other "good" hibernators such as the western jumping mouse similarly shift to this food resource because of the nutrition it provides for fat deposition (Cranford 1977). By August animals have increased their body weight by 30 to 50% and begin to enter hibernation.

Physiological and behavioral changes during hibernation are consistent with those observed in other "good" hibernators. Over 60% of an individual's life is spent in this metabolic state. Coincident with colder ambient temperatures in the autumn, burrow temperatures drop to about 10°C, and the yellow-bellied marmot lowers its body temperature to 11°C. In this condition the animal lives off its stored fat reserves until spring. In Montana, hibernation lasts until late February or early March, when the animals emerge.

Reproduction: Breeding begins on emergence of the adults in the spring. In

Montana, it would begin in late February or early March, particularly at lower elevations. Breeding lasts 2 weeks during which a high percentage of adult females mate. After a 30-day gestation period 3–8 young are produced. Weaning of young occurs as they emerge from the natal den 30 days after birth. In Montana, this occurs in early May. Most females do not reproduce until they reach 2–3 years of age. Breeding is irregular with females often skipping a year (Barash 1989).

Status: Common.

Frase, B. A., and R. S. Hoffmann. 1980. *Marmota flaviventris.* Mammalian Species 135:1–8.

Northern Flying Squirrel
Glaucomys sabrinus

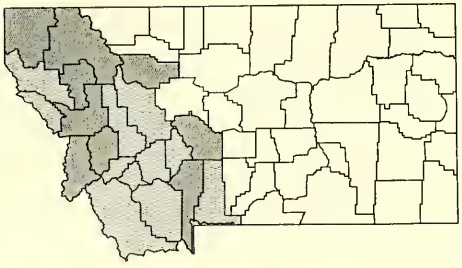
Northern flying squirrel (*Glaucomys sabrinus*).

Scientific Name: The northern flying squirrel was first described by Gmelin in 1788 from specimens obtained at the mouth of the Severn River, Ontario. Originally identified as *Sciurus hudsonius,* this designation has undergone many revisions over the past 200 years and is currently identified as *Glaucomys sabrinus.* The generic distinction, *Glaucomys,* is derived from the Greek combination, glaukos, which means "gray," and mys, which means "mouse." The specific epithet, *sabrinus,* is from the Latin term for the river Severn in England, but in this case refers to the type locality in Ontario from which the 1st specimens were collected.

Description: The northern flying squirrel is a small-bodied sciurid with noticeably large eyes; a rounded head; large, well-furred, dorso-ventrally flattened tail; and a furred patagium (flap of skin) which extends on both sides of the body from the forelegs to the hind legs connecting ankle and wrist. Body color is widely variable, although most often cinnamon to light brown above and whitish to creamy-white below. Tail ranges from light brown to black both dorsally and ventrally. Pelage is dense, long, and soft in texture. This species should not be confused with any other small mammal in the state. Large ("bug") eyes, flattened tail, and presence of patagium quickly identify these individuals. Skull characteristics readily separate the flying squirrel from ground squirrels, prairie dogs, and other tree squirrels (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 312.9(10)/♀ 321.5(10); Ta = ♂ 138.6(10)/♀ 142.0(10); HF = ♂ 40.5(10)/♀ 38.2(10); E = ♂ none/♀ 22.4(5); M [g(*n*)] = ♂ 145.5(10)/♀ 161.4(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The northern flying squirrel is widely distributed across the northern region of North America from Alaska to Newfoundland and Nova Scotia. Southern projections extend along the Pacific Coast into central California, along the Rocky Mountain chain into Wyoming and Utah, and down the Appalachian chain as far as Kentucky and Tennessee. Many dis-



Map 63. Distribution of the northern flying squirrel, *Glaucomys sabrinus*.

junct populations exist in more southern areas.

Ecology and Behavior: Throughout northern and western parts of its range the northern flying squirrel is associated with coniferous forests, predominantly white spruce, Engelmann spruce, white fir, ponderosa pine, and lodgepole pine. Populations in eastern and southeastern regions use stands of spruce and fir and deciduous forests dominated by sugar maple, red oak, and birch.

Nests are constructed either within natural cavities or abandoned woodpecker holes in dead standing trees, or they are built over limbs or within witches' brooms. Cavity nests are lined with a variety of materials from shredded bark, lichen, mosses, and grasses to fur. Similar materials are used to line nests built outside of cavities, with outer walls constructed from sticks, bark, dried grass, and lichens. The southern flying squirrel (*G. volans*; not found in Montana) will use several nests concurrently, for cache and latrine sites as well as diurnal roost sites and maternal dens (Gilmore and Gates 1985). Similar behavior is suspected in the northern flying squirrel.

A wide assortment of plants and insects are eaten by the northern flying squirrel, and small vertebrates are eaten. Fungi (both hypgeous and epigeous) and epiphytic lichens may be used heavily during certain periods of the year. The seeds of deciduous and coniferous trees are also eaten, as are insects.

The northern flying squirrel plays an integral role in the development of older-aged coniferous forests through dispersal of hypogeous mycorrhizal fungal spores. Such fungi form a mutualistic association of ectomycorrhizal rootlets with conifer species; the fungi are obligatory symbionts with these roots (Trappe and Maser 1978). Since these fungi produce fruiting bodies totally underground, they are completely dependent on mammalian mycophagists for spore dispersal, primary among which is this species.

The northern flying squirrel has a crepuscular nocturnal activity pattern foraging most often just after sundown and just before sunrise. Individuals studied at the University of Montana Biological Station on Flathead Lake have a remarkably consistent pattern of activity from one evening to the next during the summer. On exiting a nest the animal will move across its homerange quickly by gliding from tree to tree. As the animal jumps from a tree it spreads its legs to expose the patagium, thereby capturing air and providing lift for its flight (Fig. 55). Its long, broadly-flattened tail adds 20–30% to the gliding surface and effectively serves as a rudder during such a freefall. The large, forwardly-placed eyes provide excellent sight and depth perception in the relative darkness. The northern flying squirrel is particularly adept at moving through the forest in this manner. One animal leapt from a height of 30 m and maneuvered around trees during its fall by gliding back-and-forth over a lateral distance of more than 12 m, before landing on the trunk of another tree. Seconds before landing, the animal allows its hips to drop and its hindfeet to rotate forward. This accomplishes 2 things. It allows air to be trapped within the cupped patagium, quickly slowing up the animal's forward movement, and brings its feet to the front of its glide path in preparation for landing.

Once on the ground, northern flying squirrels begin a concerted effort to find foods such as the hypogeous fruiting bodies of mycorrhizal fungi, and digging intently through the forest duff. They are often so intent on this activity that one can approach

Fig. 55. Gliding behavior of the northern flying squirrel.

an animal unnoticed. Because of the large patagium stretching from fore- to hindlegs, these animals are somewhat clumsy while on the ground and are particularly vulnerable to predation at this time. When startled, they quickly seek the refuge of a nearby tree, scampering up to obtain a good vantage point, and to launch themselves across the forest.

Northern flying squirrels do not undergo torpor during winter, as does the southern flying squirrel, and can often be observed digging under the snow in search of food. Both sexes aggregate, by sex, throughout the year, often sharing a nest with 2–3 other individuals.

Reproduction: In Alberta mating in the northern flying squirrel extends from late March through May. One litter is produced yearly between May and July. Gestation lasts for 37–42 days, after which 2–4 young (range 1–6) are born. Young are weaned at 2 months and are able to glide by 3 months. Juveniles do not reach sexual maturity until 1 year of age.

Status: Common.

Wells-Gosling, N., and L. R. Heaney 1984. *Glaucomys sabrinus.* Mammalian Species 229:1–8.

Eastern Gray Squirrel
Sciurus carolinensis

Eastern gray squirrel (*Sciurus carolinensis*).

Scientific Name: The eastern gray squirrel was first described by J. F. Gmelin, in 1788, from a specimen obtained from "Carolina." This was a reference to the southeastern United States of this period. The generic designation, *Sciurus,* is from the Greek, skiouros, which is compounded from skia, meaning "shade," and oura, which means "tail;" a reference to the shading of a squirrel by its tail when sitting. The specific epithet, *carolinensis,* is a Latinized term which means "belonging to Carolina; a reference to the type locality for the original specimen.

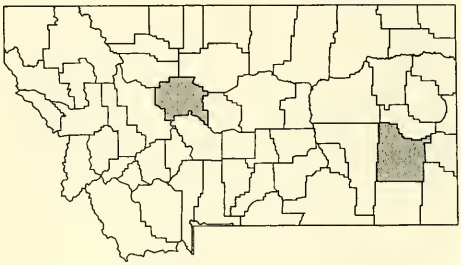
Description: The eastern gray squirrel is a medium-sized tree squirrel with a large, bushy tail. In overall appearance, it is a grizzled gray in color (hence the vernacular

name), with a diffusion of yellowish-brown hairs on its forehead, back, sides, and feet. The belly and throat region are white, as is the ring of hairs encircling the eye. Body color easily distinguishes this species from Montana's 2 native tree squirrels, the red squirrel and northern flying squirrel, and the introduced eastern fox squirrel.

Measurements: [mm(*n*); Smith 1993]: TL = ♂ 474.0(4), MT 500.0(1)/♀ 467.2(6), MT 495.0(1); Ta = ♂ 225.3(4), MT 210.0(1)/♀ 223.7(6), MT 205.0(1); HF = ♂ 64.8(4), MT 67.0(1)/♀ 66.3(6), MT 67(1); E = ♂ 28.8(4), MT 32.0(1)/♀ 28.7(6), MT 29.0(1); M [g(*n*); Smith 1993] = ♂ 463.1(4)/♀ 460.4(6), MT 694.5(1). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: As the vernacular name implies, the eastern gray squirrel is primarily found in the eastern portion of the United States. It is distributed from Maine to Florida, extending westward to a line running north to south from North Dakota through eastern Texas. Northernmost extensions enter southern portions of British Columbia, Saskatchewan, Manitoba, Ontario, Quebec, and New Brunswick, where many populations were introduced. The eastern gray squirrel has been introduced into several western states over the past several decades, 1 of which is Montana. Introductions occurred in Great Falls (Cascade County), Harlowtown (Wheatland County), and Miles City (Custer County) (Hoffmann et al. 1969). Animals brought to Harlowtown from Minnesota by a local chiropractor, in the 1960s, survived until the early 1980s (Billadeau, pers. comm.).

Ecology and Behavior: The eastern gray squirrel is most closely associated with hardwood forests, particularly with trees that provide seeds which may be easily stored over the winter [e.g., oak, maple, walnut]. In Montana, introductions have taken place in city parks where hardwood trees were previously planted. Although home ranges for the eastern gray squirrel may exceed 20 ha, most are <5 ha. Because city parks with available hardwood stands are often small, and the eastern gray squirrel is not inclined to inhabit coniferous forests in the west, introduced populations remain small in size.



Map 64. Distribution of the eastern gray squirrel, *Sciurus carolinensis*.

Nests take 1 of 2 forms, either large leaf nests constructed within a shell of twigs perched on a tree limb or dens within natural tree cavities. The former may be used more often during warmer months, particularly when individuals take up independent residence. Nests can be large, often exceeding 47 liters in volume, and are easily seen in the autumn as trees shed their leaves. Tree cavities are preferred during colder periods and may be shared by several individuals. Nests are lined from shredded tree bark, grasses, and sedges.

Seeds, nuts, flowers, and fruit of a large number of deciduous tree and shrub species are eaten by this squirrel. In Montana, food would be obtained from introduced maples and elms. Conifers, such as pines, cedar, hemlock, and spruce, provide a source of seeds as well. These may be particularly important to populations in this state. Insects, bird eggs, and nestlings may be eaten in the spring and summer.

The daily activity pattern is bimodal during the spring, summer, and autumn, with peaks 2 hours after sunrise and 2–5 hours before sunset. During colder months activity is concentrated around a single time peaking 2–4 hours before sunset. Animals spend time foraging, grooming, and resting, efforts allocated to each of these behaviors

shifting with the season and the local food supply. Although group nesting occurs within and between sexes, a distinct hierarchy develops among members of a social group, with agonistic behaviors being displayed. One of the most common reasons for introducing this species has been the enjoyment which people derive from watching squirrels.

The food storage activity which this species exhibits in autumn, and for which it is well-known, is referred to as "scatter hoarding." Nuts are gathered from around the animal's home range and buried 2 cm deep. This behavior provides dispersed food caches which are less susceptible to theft from competitors. Animals can remember where nuts have been deposited, although olfaction plays an important role too.

Throughout its native range in the eastern United States, the eastern gray squirrel is often found in sympatry with the red squirrel, the common native species of Montana. Where this occurs the 2 species are somewhat segregated, with gray squirrels more dominant in hardwood forests and red squirrels dominant in coniferous stands. Although considerable overlap exists in diet, habitat specializations appear to determine the differences in their distributions. Eastern gray squirrels are better adapted to eat hardwood nuts, while red squirrels are better adapted to eating conifer seeds.

Reproduction: The eastern gray squirrel has 2 breeding seasons, the 1st between December and February, and the 2nd between June and July. Females in estrus attract numerous males and may breed with several; the dominance hierarchy which forms between males is overtly seen as extensive chases between individuals. After a gestation period of 44 days a litter of 2–3 young is born. Weaning, which begins at 7 weeks, is completed by the 10th–12th week. A small percentage of females in southern Canada can breed at the end of their 1st summer (if born early in the spring), at an age of 7–9 months. However, most will not breed until they are at least 15 months old.

Status: Introduced into the state. Populations exist in Great Falls, Harlowton, and Miles City.

Koprowski, J. L. 1994. *Sciurus carolinensis.* Mammalian Species 480:1–9.

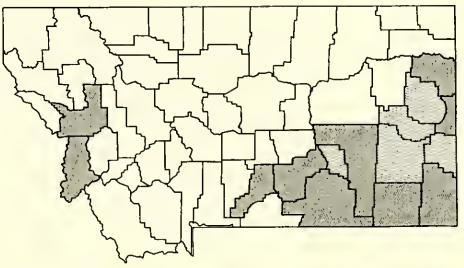
Eastern Fox Squirrel
Sciurus niger

Eastern fox squirrel (*Sciurus niger*).

Scientific Name: The eastern fox squirrel was first described by Carolus Linnaeus, in 1758, from specimens collected in what is today southern South Carolina. Although many changes have occurred in the scientific nomenclature of this species over the past 2 centuries, the currently accepted designation, *Sciurus niger,* is as Linnaeus proposed. The generic designation, *Sciurus,* is from the Greek, skiouros, which is compounded from skia, which means "shade," and oura, which means "tail;" a reference to the shading of a squirrel by its tail when sitting. The specific epithet, *niger,* is Latin meaning "black;" a reference to the color of the original specimen.

Description: The eastern fox squirrel is a medium- to large-sized tree squirrel, with a long, bushy tail. In body size, it is the largest tree squirrel in Montana. Weights are nearly double that of the eastern gray squirrel, and 4–8 times the weight of native red squirrels and northern flying squirrels. Although body color varies throughout the United States, from a grizzled buff-orange to silvery-gray and even black, populations found in Montana all

have a grayish, grizzled, dorsal pelage with a definite orangish tinge. The belly fur is orangish-white. The vernacular name refers to the fact that the color pattern resembles that of the red fox. The larger body size, and distinctive color, clearly distinguishes the eastern fox squirrel from other tree squirrels in the state.



Map 65. Distribution of the eastern fox squirrel, *Sciurus niger.*

Measurements: [mm(*n*)]: TL = ♂ 488.3(3)/♀ 556.5(2); Ta = ♂ 227.0(3)/♀ 249.5(2); HF = ♂ 64.5(2)/♀ 63.5(2); E = ♂ 25.3(3)/♀ 25.0(2); M [g(*n*)] = ♂ 756.4(4)/♀ 467.0(4). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The eastern fox squirrel is distributed throughout the eastern United States, with the exception of the northeastern most region, from New Jersey and eastern New York northward. In the west, its range extends from southeastern Saskatchewan, through western Texas, with extensions into Montana and Mexico. After reintroduction efforts in North Dakota, in 1941 (Hibbard 1956), the eastern fox squirrel expanded its range westward along the Yellowstone River into Big Horn, Stillwater, and Yellowstone counties of Montana (Hoffmann et al. 1969). This expansion now includes populations along the Powder River, Powder River County and Tounge River, Rosebud County (Knapp and Swenson 1986), and a tributary of the Little Missouri River, Wibaux County (Matthews and Swenson 1982). The eastern fox squirrel also has been introduced into the cities of Missoula, Missoula County and Hamilton, Ravalli County.

Ecology and Behavior: The eastern fox squirrel inhabits deciduous or mixed coniferous–deciduous forests throughout its range. Natural extensions in Montana have followed cottonwood stands along riparian bottomlands (Knapp and Swenson 1986); reintroductions have been successful where introduced hardwoods exist in city parks. This habitat association is tightly tied to the availability of nuts, flowers, seeds, and tree buds of many deciduous species, notable among which are oaks, maples, elms, and cottonwood. Native eastern populations eat the seeds of several coniferous species. Although such a seed diet is preferred, the eastern fox squirrel can eat a wide variety of plant and even animal materials (specifically insects, birds, and bird eggs).

Fox squirrels use 1 of 2 types of nests throughout the year, either leaf nests or natural tree cavities. Leaf nests (termed "drays"), constructed from twigs and leaves, and perched on tree limbs, are primarily used during the warmer months. As winter approaches, individuals move into den cavities which have greater protection from the cold. Both nest forms are lined with shredded bark or leaf material to provide a soft inner nest. Summer leaf nests may be easily seen in autumn, perched at the tops of trees, as canopy foliage is lost. Several nests may be used throughout the year.

The daily activity pattern of the eastern fox squirrel is similar to that of the eastern gray squirrel. Spring, summer, and autumn activity begins just after sunrise with an early morning peak 2 hours later. A 2nd peak occurs 2–4 hours before sunset. During the warmest months a 3rd peak may occur at midday. A unimodal pattern is adopted during the colder winter months, with greatest activity around midday. As with the eastern gray squirrel, the eastern fox squirrel is a scatter hoarder, collecting nuts throughout summer and autumn and burying them throughout its home range in a randomly

dispersed fashion. Such a hoarding strategy may reduce loss to competitors. A high percentage of buried nuts are relocated when needed, probably through both memory and olfactory cues.

Many eastern states have attempted to manage the eastern fox squirrel for public hunting and for viewing. Interestingly, squirrels are considered to be 2nd only to songbirds in importance for viewing and as subjects for nature photography.

Reproduction: The breeding season is similar to that of the eastern gray squirrel with 2 reproductive periods each year. The 1st is between November and February, with most activity in December, and the 2nd is between April and July with peak activity in June. Montana populations may run slightly later due to the more northern latitude. Several males may mate with a female, following a dominance hierarchy. After a gestation of 45 days an average litter of 2–3 young will be born. Although 2 breeding periods occur each year, each successful female produces only 1 litter. Weaning, which begins at 8 weeks, is completed by 12 weeks. Males reach sexual maturity at 10–11 months; females develop more slowly attaining sexual maturity at 15 months.

Status: Locally common in eastern Montana where their range is expanding along the Yellowstone River and its tributaries, and the Little Missouri River. The introduced population in Missoula is well established.

Koprowski, J. L. 1994. *Sciurus niger*. Mammalian Species 479:1–9.

Red Squirrel
Tamiasciurus hudsonicus

Red squirrel (*Tamiasciurus hudsonicus*). See plate 7.

Scientific Name: The red squirrel was first described by Erxleben, in 1777, from specimens obtained near the mouth of the Severn River, Ontario. Initially designated *Sciurus vulgaris hudsonicus*, the current name was applied, in 1923, by Pocock. The generic distinction *Tamiasciurus* is from the Greek combination tamias, which means "a storer," and skiouros, which is compounded from skia, meaning "shade," and oura, meaning "tail;" references to hoarding behavior, and the shading of a squirrel by its tail when sitting, respectively. The specific epithet, *hudsonicus*, identifies the type locality of Hudson Bay from which the red squirrel was first described.

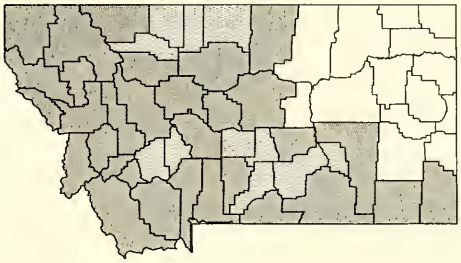
Description: The red squirrel is a small, compact tree squirrel, only slightly larger (although somewhat heavier) than Montana's other native tree squirrel, the northern flying squirrel. Although the vernacular name implies that this species is red, many populations are not this color but instead are predominantly brown. If a red hue is apparent, it is washed through the

darker brown coat on back and sides. A distinct white eye ring exists. The venter is white and the tail is reddish-brown above and grayish to yellowish below. Red squirrels molt twice a year; winter pelage is often more colorful (this depends on the population), with a much more pronounced red stripe of hairs running along the dorsal surface. The rest of the coat may be shaded with more gray than is found in the summer. Most Montana populations have a distinct lateral black line separating dorsal brown and ventral white hair. Ears are prominent, haired, and capped with sharp brown tufts during winter. The red squirrel should not be confused with any other tree squirrel in Montana. In body conformation and color, it is distinctly separate from the northern flying squirrel. Body size and color also clearly distinguish the red squirrel from both reintroduced species, the fox squirrel and the gray squirrel.

Measurements: [mm(*n*)]: TL = ♂ 326.8(10)/♀ 328.0(10); Ta = ♂ 115.9(10)/♀ 125.0(10); HF = ♂ 44.6(10)/♀ 47.6(10); E = ♂ none/♀ 22.0(4); M [g(*n*)] = ♂ 238.3(10)/♀ 239.4(10). Dental formula: i 1/1, c 0/0, p 1/1, m 3/3, total 20.

Distribution: The red squirrel is extensively distributed from northwestern Alaska, across all Canadian provinces, and into the continental United States along 2 paths. In the central and eastern United States, populations extend from eastern North Dakota to the east coast, as far southward as Tennessee and the Carolinas. In the west, populations from British Columbia and Alberta extend through Washington, Idaho, and Montana, to New Mexico and Arizona.

Ecology and Behavior: The red squirrel is 1 of the most common small mammals in the state, using diverse habitats along a wide moisture and elevational gradient. In western regions, it ranges from lower elevation montane forests of ponderosa pine and Douglas fir, up to subalpine



Map 66. Distribution of the red squirrel, *Tamiasciurus hudsonicus*.

Engelmann spruce–subalpine fir communities. In the east, it is associated with drier ponderosa pine.

The red squirrel is a cavity nester, preferring woodpecker cavities in ponderosa pine, where available. In spruce–fir forests fewer cavities exist and under these conditions a large nest of grasses is constructed on a branch close to the trunk. Within such a grass structure, the nest cavity is thickly insulated with moss, lichens, and shredded grass or bark. Unlike the northern flying squirrel, the red squirrel uses only 1 nest at a time. Foraging occurs in a radius out from the nest site during the day. During warmer months, most activity occurs early morning, or late afternoon. In the winter, activity is centered toward midday, when most light, and thus, warmth is available (Fig. 56). Although conifer seeds (particularly spruce and pine) are highly preferred, the red squirrel is a true omnivore, feeding on a variety of seeds, nuts, berries, flowers, fungi, invertebrates, birds (nestlings and bird eggs), and even small mammals. Rather than "scatter hoarding," as fox and gray squirrels do, the red squirrel concentrates on collecting and storing large numbers of cones in a central locality (a behavior termed "larder-hoarding"). Such cone caches, referred to as "middens," may accumulate in huge piles on stumps or logs, providing the animal with a convenient larder on which to dine. A midden site may be used over several years becoming enormous in size; measurements of 3 by 11 m, and 46 cm in depth are not uncommon.

Fig. 56. A radiocollared red squirrel.

Several such middens may be produced by a single animal over the course of a summer or autumn. These food caches are highly prized and defended aggressively. When disturbed or challenged, a distinctive chatter call is produced warning the intruder away. More vigorous display behaviors (tail shaking and movement back and forth on a limb) may occur if the vocal warning goes unheeded, and extensive chases may ensue if all else fails.

As with other tree squirrels, the red squirrel is active year-round, relying on its seed caches for sustenance. During extreme cold spells, it may remain in its well insulated tree nest. Stable population densities are maintained from 1 year to the next, primarily through the development and defense of territories based on food supplies. New individuals entering the population are forced to disperse over the available habitat, in relation to the food supply, thus allowing individuals "... optimum conditions for harvesting, storing, and defending a seasonal food supply so that it will be available throughout the year" (Smith 1968:61).

Reproduction: Breeding begins in March or April and may extend over 3–4 months. When a female comes into heat, several males will congregate on her territory and attempt to establish dominance. Aggressive chasing behavior, and actual physical fighting, ultimately determines the dominant male. This individual will then follow the estrous female for the better part of the day, copulating with the female, and continually fending off subdominant males. Gestation lasts for 33 days after which 1 to 8 ($\bar{x}$ = 2.88–3.75) young are born. In Montana, as in British Columbia and Alberta, only 1 litter/year is produced. Second litters are possible although rare, and are due to exceptionally high-quality food supplies at the time of conception.

Young are slow to develop; they are hairless at birth with eyes and ears closed. The external auditory meatus opens at day 18, at which time young will respond to sound; eyes open at 4 weeks. Young venture out from the nest beginning at 7 weeks and are completely weaned 1–2 weeks later. Sexual maturity is attained in the spring of the 2nd year following birth, at 1 year of age.

Status: Common.

Steele, M. A. 1998. *Tamiasciurus hudsonicus.* Mammalian Species 586:1–9.

Uinta Ground Squirrel
Spermophilus armatus

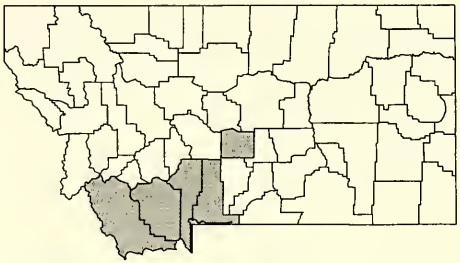
Scientific Name: The Uinta ground squirrel was first described in 1863, by Robert W. Kennicott, from specimens obtained from the foothills of the Uinta Mountains, near Fort Bridger, Wyoming. Kennicott was a naturalist and explorer who co-founded the Chicago Academy of Sciences. The genus distinction, *Spermophilus,* is from the Greek combination, sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The species epithet, *armatus,* is apparently from the Latin, armatus, which means "armed." Why Kennicott applied this name is unclear.

Description: The Uinta ground squirrel is a medium-sized ground squirrel, identified by its grayish-brown dorsal and lateral color. Head is gray with a cinnamon cast, and with the appearance of a gray collar. Hind legs have a cinnamon cast, while feet are a pinkish-buff. The gray underside of the tail is a distinctive characteristic. No striping occurs. This species closely resembles Richardson's ground squirrel. The Uinta ground squirrel is, however, somewhat larger and can be distinguished by its darker gray color. Richardson's ground squirrel is lighter and has a buffy-cinnamon cast to the venter of its tail.

Measurements: [mm(*n*)]: TL = ♂ 303.1(10)/♀ 275.3(8); Ta = ♂ 74.3(10)/♀ 65.1(8); HF = ♂ 46.1(10)/♀ 41.4(8); E = ♂ 16.3(4)/♀ 14.3(4); M [g(*n*)] = ♂ none/♀ 347.9(3). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The Uinta ground squirrel is relatively limited in the intermountain west, extending from southwestern Montana, through southeastern Idaho and western Wyoming, into the north central portion of Utah.

Ecology and Behavior: The range of the Unita ground squirrel lies within that of Richardson's ground squirrel and the Columbian ground squirrel. Although, in general appearance, the Uinta ground squirrel is more similar to Richardson's ground squirrel, in habitat preference it reflects the Columbian ground squirrel. Preference is given to the open grassy habitats found in subalpine meadows nearby forest edges. Aspen groves are common habitat, but Uinta ground squirrels are more often associated with the grass openings.



Map 67. Distribution of the Uinta ground squirrel, *Spermophilus armatus.*

Burrows are similar to those of other ground squirrels. Adult males and females do not share their burrows, and once young disperse they no longer associate with their mother. The social system is an aggregation of individuals living as isolates. Yearly activity is highly compressed around the spring and early summer, with the remainder of the year spent in hibernation. Most populations exist at higher elevations where favorable weather conditions are short lived. Emergence from hibernation begins during the latter part of March and the 1st week in April. Adult males appear 1st, followed by adult females, yearling females, and yearling males, in that order, over a several week period. Following breeding, males spend a majority of time foraging in an attempt to replenish fat stores for the next period of hibernation. Males and females gain weight quickly in early summer and begin to hibernate in mid-July. Juveniles, born in early

summer, must continue to grow and deposit fats and as such do not hibernate until early September.

Green vegetation is highly preferred with leaves of grasses and forbs being replaced by their seeds as the season progresses. The latter foods provide needed oils which are converted into body fats to support hibernation.

Following breeding, adult males move away from female territories and remain isolated. They rarely interact, even antagonistically, with other members of the population. Females, having weaned their young, spend a majority of their above ground time foraging away from their natal burrow. A long-term study in Utah has observed that post-reproductive females seek brushy habitats away from their burrows, possibly in an attempt to find cooler temperatures.

Reproduction: Breeding begins in spring 1 to 2 weeks after males emerge, and just as females are emerging. Most females mate within 2–4 days. Quickly thereafter, pregnant females become territorial around their hibernation burrows, which now serve as the birthing den. Gestation is 23–26 days in length. A mean litter size of 5.4 (4–8) was noted in Utah. Young appear above ground at about day 22 where they begin to explore their surroundings and taste their 1st grass. A few days prior to emergence of newborns, the mother constructs a new entrance for the burrow which the young will use. This entrance is developed from below ground and opens at some distance from the original entrance. The opening is not used by the female until several days after the young emerge; it is primarily for the young and is less apparent than that used throughout the spring by the adult. This behavior is likely an anti-predator protection for juveniles as they are vulnerable when they 1st appear. The new openings also exit in areas less grazed by adults. These areas may provide a ready food source for juveniles without the necessity of their traveling far from the protection of the entrance.

Status: Common, although never abundant.

Eshelman, B. D., and C. S. Sonnemann. 2000. *Spermophilus armatus*. Mammalian Species 637:1–6.

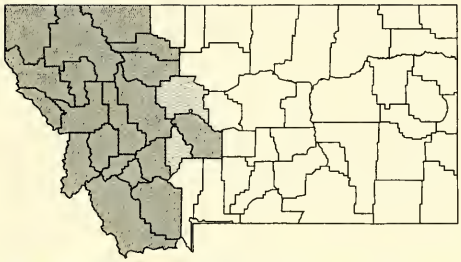
Columbian Ground Squirrel
Spermophilus columbianus

Columbian ground squirrel (*Spermophilus columbianus*). See plate 7.

Scientific Name: The Columbian ground squirrel was first described by George Ord, in 1815, based on Lewis and Clark's original descriptions of specimens between the Clearwater and Lochsa rivers, in northeastern Idaho. Originally identified as *Arctomys columbianus,* the current usage, *Spermophilus columbianus,* was first proposed by C. Hart Merriam, and L. Stejneger, in 1891. The generic designation, *Spermophilus,* is derived from the Greek combination, sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The specific epithet, *columbianus,* is a Latinized usage referring to the Columbia River along which Lewis and Clark had been exploring.

Description: The 1st scientific description of the Columbian ground squirrel was made by Meriwether Lewis on 27 May 27 1806, as his party camped at the present location of Kamiah, Idaho (Lewis and Clark's Camp Chopunnish). His description, as concise and accurate today as it was nearly 200 years ago, is excerpted here.

> "There is a species of Burrowing squirrel common in these plains which in their habits somewhat resemble those of the missouri [here he refers to Richardson's ground squirrel] but are a distinct species. this little animal measures one fot five and ½ inches from the nose to the extremity of the tail, of which the tail occupys 2 ¼ inches only; in the girth it is 11 In. the body is proportionably long, the neck and legs short; the ears are short, obtusely pointed, and lie close to the head; the aperature of the ear is larger proportionably than most animals which burrow. the eyes are of moderate size, the puple black and iris of a dark sooty brown. the teeth are like those of the squirrel as is it's whole contour. the whiskers are full, long and black; it also has some long black hairs above the eyes. it has five toes on each foot; the two inner toes of the fore feet are remarkably short, and have short blunt nails. the remaining toes on those feet are long, black, slightly curved, and sharply pointed. the outer and inner toes of the hind feet are not short yet they are by no means as long as the three toes in the center of the foot which are remarkably long but the nails are not as long as those of the fore feet tho' of the same form and colour. the hair of the tail tho' thickly inserted on every part rispects the two sides only. this gives it a flat appearance and a long oval form. the tips of the hair which form the outer edges of the tail are white. the base of the hairs are either black or a fox red. the lower part of the jaws, under part of the neck, legs and feet from the body down and belley are of a light brick red.



Map 68. Distribution of the Columbian ground squirrel, *Spermophilus columbianus*.

the nose as high as the eyes is of a darker brick red. the upper part of the head neck and body are of a curious brownish grey colour with a cast of the brick red. the longer hair of these parts being of a redish white colour at their extremities, fall together in such a manner as to give it the appearance of being speckled at a little distance." (Moulton 1991:291–292).

Of 5 other species of ground squirrel found in Montana, the Columbian ground squirrel may be confused with 3, the Uinta ground squirrel, Richardson's ground squirrel, and the Wyoming ground squirrel. It is best differentiated from these species by its spotted–mottled pelage, the others are of solid color. The Columbian ground squirrel is also somewhat larger with a hind foot measurement of >48 mm; all others have hind feet <48 mm.

Measurements: [mm(*n*)]: TL = ♂ 347.5(10)/♀ 337.9(10); Ta = ♂ 91.6(10)/♀ 94.7(10); HF = ♂ 50.7(10)/♀ 48.8(10); E = ♂ 18.3(10)/♀ 17.3(10;) M [g(*n*)] = ♂ 536.9(10)/♀ 457.2(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The Columbian ground squirrel has a relatively narrow range extending from northeastern British Columbia, southward along the Canadian Rocky Mountains, into western Montana. Further extensions occur across the northern half of Idaho, eastern Washington, and the northeastern corner of Oregon.

Ecology and Behavior: Although the Columbian ground squirrel is primarily associated with subalpine to alpine meadows in more western regions, particularly where moist conditions exist, it may also be found in Montana at lower elevations, in more open woodlands. It may be readily observed in the intermontane valleys of western Montana at elevations as low as 1,000 m.

Burrow systems are typically constructed with several openings leading into horizontal tunnels which lie 38 to 79 cm deep. Openings are most often small and nondescript (unlike those of the prairie dog) and may be incorporated into a boulder field, as is typical at higher elevations such as in Glacier National Park. At lower elevations, in more open habitats, larger, funnel-shaped openings may be seen. Single nest chambers are often large (0.3–0.6 m in diameter) and filled with shredded leaves and grass. Additional chambers may be constructed to serve as toilet sites. Food storage chambers are not typical, as Columbian ground squirrels hibernate. Some individuals, however, store bulbs for possible use in spring, before fresh vegetation is available. Columbian ground squirrels have a well-developed, colonial, social structure; many burrows may exist in a meadow with adult males and females overlapping in their home ranges.

Foraging activity is greatest in the morning and late afternoon when temperatures are warm but not hot. A variety of plant species in all stages of development are consumed; bulbs, fruits, and seeds are eaten, as are flowers, and green vegetation such as bluebunch wheatgrass, clover, and dandelions. Montana populations also eat the green vegetation of beargrass, balsamroot, silky lupine, and willow and the bulbs of camas, glacier lily, and wild onion.

Columbian ground squirrels are "central place foragers" meaning they selectively forage out from their burrow in a radius. After the availability of preferred food items close to the burrow decreases, the animals must forage at further distances. Trade-offs must be made with this type of feeding strategy because, as the distance traveled increases,

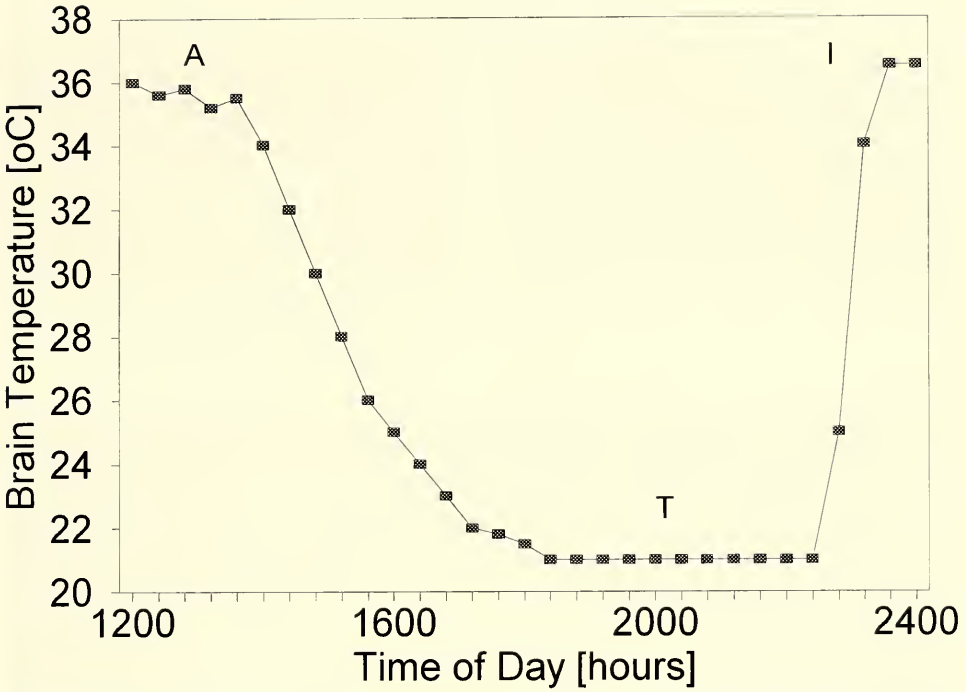


Fig. 57. Pattern of hibernation activity as shown by recording of animal's core body temperature throughout hibernation (A = active, T = torpor, I = intertorpor period).

so does the risk of predation. Between foraging bouts, animals may sun themselves, although they are always alert to predators. Animals routinely sit upright at their burrow entrances and search for intruders. If a predator is sighted, an alarm call is made consisting of a shrill chirp. Other animals in the colony will immediately respond by scampering into their burrows.

Feeding activities intensify, as autumn approaches, in anticipation of pending hibernation. Within the last few weeks above ground, significant weight gains are made. Total body weight then levels off and may even slightly decline. Timing of entrance into hibernation is influenced by elevation of the colony site and prevailing environmental conditions. Populations living at lower elevations remain active 2 weeks longer than those living at higher elevations (Dobson et al. 1992). This difference is in part due to the shorter availability of resources at the latter sites. In Montana, individuals enter hibernation during the 1st week of August. Initial torpor bouts are shallow and of short duration. As autumn progresses, these bouts become more significant; body temperatures drop to lower and lower levels and are maintained at these levels for longer periods of time. By winter, torpor bouts last 20–30 days, with body temperatures approaching 1°C (Fig. 57). The depth and insulation of the nest cavity maintains an environment which is just above freezing. Periodic arousals occur throughout hibernation allowing animals to rewarm for short periods (often no more than 1–2 hours). During these periods of activity, the kidneys again become functional, and the nitrogenous wastes, which have built up in the body, can be removed. As spring approaches, torpor bouts become shallower and shorter in duration. In Montana, animals emerge as early as mid-April, depending on spring temperatures and snow depth. Adult males emerge 1st fol-

lowed by adult females. Juveniles of both sexes emerge later than adults.

Columbian ground squirrels spend nearly 9 months of the year hibernating. During this period the animal is totally dependent on stored body fats for energy, thus, on emergence, individuals have lost significant amounts of weight and need to begin foraging immediately. Overwinter mortality may be high if spring is delayed and green vegetation is late in appearing.

Reproduction: Breeding begins in spring immediately on emergence from hibernation. Adult males are 1st to emerge in anticipation of receptive females. Testicular development begins late in hibernation so that at emergence adult males are fully reproductive. Reproductive development in adult females also begins before emergence so that estrus is reached quickly thereafter. Breeding activity in a colony may span 2–3 weeks. Gestation lasts for 24 days; average litter sizes range from 2.1–4.2. A single litter is produced yearly. Young are weaned in 30 days but do not attain sexual maturity until 2 (females) to 3 (males) years.

Status: Common.

Elliott, C. L., and J. T. Flinders. 1991. *Spermophilus columbianus*. Mammalian Species 372:1–9.

Wyoming Ground Squirrel
Spermophilus elegans

Scientific Name: The Wyoming ground squirrel was first described by Robert W. Kennicott, in 1863, from specimens obtained near Ft. Bridger, Uinta County, Wyoming. Kennicott founded the Chicago Academy of Sciences and served as Chief of Scientific Corps for the Russian Overland International Telegraph Expedition. In this position, he did extensive naturalist surveys in northwestern Canada and Alaska. In 1938, Howell grouped *S. elegans* with *S. richardsonii*, and for more than 20 years the 2 were considered conspecific. However, over the past 30 years a number of morphological, behavioral, and genetic studies support original species distinction. Thus, the name originally proposed by Kennicott is accepted today. The genus designation, *Spermophilus*, is derived from the Greek combination, sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The specific epithet, *elegans*, is Latin for "neat" or "elegant."

Description: The Wyoming ground squirrel is a small- to medium-sized ground squirrel with short, rounded ears; large feet with strong claws; and a relatively short tail. It has a solid color of light brown, with a grayish cast on head, neck, and shoulders. Ventral color has a yellowish tinge, although is still predominantly grayish in appearance. Tail continues the light brown of body pelage, with black guard hairs tipped in white, and a more orangish-buff shade on ventral surface. The Wyoming ground squirrel may be confused with the Uinta ground squirrel, and Richardson's ground squirrel. Color of the ventral surface of the tail can be used to separate the Wyoming ground squirrel from the Uinta ground squirrel; in the latter it is gray. However, the Wyoming ground squirrel and Richardson's ground squirrel cannot be distinguished by color alone. Hind foot length, greatest skull length, and length of toothrow are all smaller for the Wyoming ground squirrel (Foresman 2001).

Measurements: [mm(n); ear measurements from Armstrong 1972]: TL = ♂ 289.0(3)/♀ 283.0(1); Ta = ♂ 62.0(3)/♀ 71.0(1); HF = ♂ 45.5(3)/♀ 45.0(1); E = ♂ 10.0(2)/♀ 12.0(10); M [g(n); Armstrong 1972] = ♂ none/♀ 274.7(3). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Northern water shrew (*Sorex palustris*). See species account, page 29.

Vagrant shrew (*Sorex vagrans*). See species account, page 32.

Pallid bat (*Antrozous pallidus*). See species account, page 37.

Big brown bat (*Eptesicus fuscus*). See species account, page 41.

Hoary bat (*Lasiurus cinereus*). See species account, page 47.

Pika (*Ochotona princeps*). See species account, page 62.

Snowshoe hare (*Lepus americanus*) in winter pelage. See species account, page 66.

Black-tailed jackrabbit (*Lepus californicus*). See species account, page 68.

Mountain cottontail (*Sylvilagus nuttallii*). See species account, page 75.

Beaver (*Castor canadensis*). See species account, page 78.

Porcupine (*Erethizon dorsatum*). See species account, page 83.

Northern pocket gopher (*Thymomys talpoides*). See species account, page 87.

Southern red-backed vole (*Clethrionomys gapperi*). See species account, page 96.

Long-tailed vole (*Microtus longicaudus*). See species account, page 100.

Meadow vole (*Microtus pennsylvanicus*). See species account, page 104.

Water vole (*Microtus richardsoni*). See species account, page 106.

Bushy-tailed woodrat (*Neotoma cinerea*). See species account, page 110.

Northern grasshopper mouse (*Onychomys leucogaster*). See species account, page 115.

Deer mouse (*Peromyscus maniculatus*). See species account, page 118.

House mouse (*Mus musculus*). See species account, page 121.

Northern bog lemming (*Synaptomys borealis*). See species account, page 125.

Black-tailed prairie dog (*Cynomys ludoviscianus*). See species account, page 130.

Hoary marmot (*Marmota caligata*). See species account, page 133.

Yellow-bellied marmot (*Marmota flaviventris*). See species account, page 135.

Red squirrel (*Tamiasciurus hudsonicus*). See species account, page 144.

Columbian ground squirrel (*Spermophilus columbianus*). See species account, page 149.

Golden-mantled ground squirrel (*Spermophilus lateralis*). See species account, page 154.

Yellow-pine chipmunk (*Tamias amoenus*). See species account, page 160.

Red-tailed chipmunk (*Tamias ruficaudus*). See species account, page 163.

Western jumping mouse (*Zapus princeps*). See species account, page 169.

Coyote (*Canis latrans*). See species account, page 174.

Wolf (*Canis lupus*). See species account, page 177.

Red fox (*Vulpes vulpes*). See species account, page 181.

Mountain lion (*Puma concolor*). See species account, page 183.

Lynx (*Lynx canadensis*). See species account, page 186.

Bobcat (*Lynx rufus*). See species account, page 189.

Striped skunk (*Mephitis mephitis*). See species account, page 191.

Northern river otter (*Lontra canadensis*). See species account, page 199.

Black-footed ferret (*Mustela nigripes*). See species account, page 211.

American marten (*Martes americana*). See species account, page 201.

Raccoon (*Procyon lotor*). See species account, page 218.

Black bear in brown color phase (*Ursus americanus*). See species account, page 220.

Grizzly bear (*Ursus arctos*). See species account, page 224.

Pronghorn buck (*Antilocapra americana*). See species account, page 229.

Bison bull (*Bos bison*). See species account, page 232.

Mountain goat male (*Oreamnos americanus*). See species account, page 236.

Bighorn sheep ram (*Ovis canadensis*). See species account, page 238.

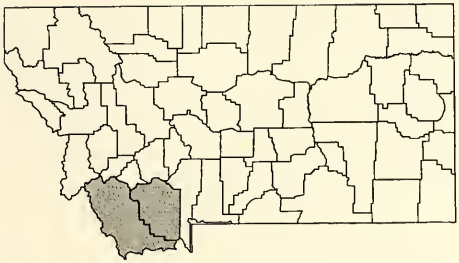
Bull moose (*Alces alces*). See species account, page 240.

Bull elk (left), cow (right), juvenile (center) (*Cervus elaphus*). See species account, page 243.

Plate 16

Mule deer (*Odocoileus hemionus*) buck (center and right) and doe (left). See species account, page 246.

White-tailed deer (*Odocoileus virginianus*) buck at rest (left) and "flagging" (right). See species account, page. See species account, page 249.



Map 69. Distribution of the Wyoming ground squirrel, *Spermophilus elegans*.

Distribution: The Wyoming ground squirrel is found in 3 disjunct regions of the intermountain northwest spread between Montana, Idaho, Oregon, Nevada, Wyoming, and Colorado, with small extensions into Utah and Nebraska.

Ecology and Behavior: The Wyoming ground squirrel has a fairly wide habitat tolerance and occurs from low elevation grassland and sagebrush regions, to higher elevation montane meadows and even subalpine slopes. The Wyoming ground squirrel replaces the Columbian ground squirrel at higher elevations as you proceed south of the latter species' distribution. In southwestern Montana, near Harrison (Madison County), the Wyoming ground squirrel lives in the same colony with Columbian, Richardson's, and Uinta ground squirrels. Colonies are formed in suitable habitat, but colony members live independently. Population densities vary depending on available habitat and time of year. Peak numbers are reached in June when juveniles first emerge; values as high as 48/ha have been recorded in montane meadows.

Activity patterns are strictly diurnal and bimodal, with peak periods during midmorning and early evening. Only about 3 hours are spent above ground daily. Such an activity pattern is a behavioral response to compensate for physiological limits in the Wyoming ground squirrel's thermoregulatory abilities. Detailed physiological and behavioral studies have demonstrated that if the Wyoming ground squirrel is exposed to extended periods of elevated ambient temperatures it will experience lethal hyperthermia (Byman 1985). Other species, such as Belding's ground squirrel, offset heat gains by adjusting their posture to orient themselves with respect to the direction of solar radiation in such a manner as to lessen heat absorption (Morhardt and Gates 1974).

Foraging accounts for about 39% of the above ground time and centers around a variety of forbs and grasses. Little preference is shown as the animal grazes. The Wyoming ground squirrel can eat plants, such as vetches, which are poisonous to cattle. Such toxic materials are diluted by the variety of other plants eaten during a feeding.

Hibernation in the Wyoming ground squirrel is, in most respects, similar to that of Columbian and Richardson's ground squirrels. Emergence occurs in late March to early April (depending on latitude and elevation), and entry into hibernation begins in late July, thus only 4 months are spent in the non-hibernatory state. Juveniles remain above ground for an additional month because they have less time to gain the required fat stores.

Many diseases have been identified in *S. elegans* populations, notable among these is sylvatic plague. As in prairie dogs, this disease may nearly decimate a ground squirrel colony. Disease concerns and competition with livestock for grasses has led to concerted efforts to eradicate this species from rangelands.

Considered to be a relatively asocial ground squirrel, colony structure is described as "single-family, female kin clusters." Adult males and females are only together for the short period surrounding breeding. Following breeding adult home ranges do not overlap. Initially juveniles of both sexes live with their mother and do not socialize with other individuals. By August, juvenile males disperse from their natal site, although, juvenile females may remain in, or near, this site for life.

Reproduction: The breeding season coincides with emergence from hibernation.

Reproductive development in both adult males and females begins prior to emergence, such that breeding occurs 1–4 days thereafter. Gestation is 22 days. Litters in captivity averaged 7 young. Weaning occurs between 4 and 6 weeks, and both males and females may reach sexual maturity as yearlings.

Status: Locally common.

Zegers, D. A. 1984. *Spermophilus elegans.* Mammalian Species 214:1–7.

Golden-mantled Ground Squirrel
Spermophilus lateralis

Golden-mantled ground squirrel (*Spermophilus lateralis*). See plate 8.

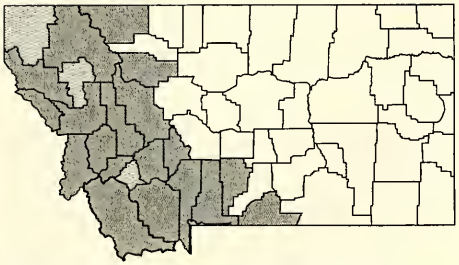
Scientific Name: The golden-mantled ground squirrel was first described by Thomas Say, a highly respected naturalist, in 1823, from specimens obtained near Canyon City, Fremont County, Colorado. Originally identified as *Sciurus lateralis,* the current usage was applied by Cuvier in 1831. The generic designation, *Spermophilus,* is derived from the Greek combination sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The specific epithet, *lateralis,* refers to the lateral black and white stripes which this species exhibits.

Description: The golden-mantled ground squirrel is easily identified by its golden brown head and shoulders, the "mantle" from which it receives it vernacular name, and distinct white lateral stripes bordered by black stripes. Below the striping, which runs from shoulders to tail, the fur is yellowish-white; the ventral surface ranges from white to yellowish-gray. Dark eyes are set off by a ring of white hairs. This species should not be confused with any other Montana ground squirrel. Its distinctive body color separates it from all other *Spermophilus.* From a distance it might be mistaken for a chipmunk (*Tamias*) due to the similarity in lateral striping, however, stripes of the golden-mantled ground squirrel do not extend through the eyes.

Measurements: [mm(*n*)]: TL = ♂ 280.3(10)/♀ 270.3(10); Ta = ♂ 95.3(10)/♀ 90.9(10); HF = ♂ 42.2(10)/♀ 41.2(10); E = ♂ none/♀ 23.2(5); M [g(*n*)] = ♂ 202.0(10)/♀ 203.1(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The golden-mantled ground squirrel is found throughout the mountainous regions of the western United States and Canada extending from central British Columbia and Alberta, to New Mexico and Arizona. In east–west distribution it extends from central Colorado, to the Oregon and California coast.

Ecology and Behavior: The golden-mantled ground squirrel is common in western Montana forests in a wide range of habitats from intermontane valleys to alpine rock slopes. It is associated with ponderosa pine, lodgepole pine, Engelmann spruce,



Map 70. Distribution of the Golden-mantled ground squirrel, *Spermophilus lateralis.*

and Douglas fir stands, particularly where openings exist. It readily uses fragmented or disturbed sites if rock or brush cover is available. It will quickly invade burned or logged sites, and may be seen perched on a tree stump. Burrows are constructed under logs or at the base of stumps and within rocky outcroppings. Several entrances access the tunnel system which may lie up to 1 m underground and extend up to 2 m in length. Nests are formed from dried, shredded grasses and leaves.

The golden-mantled ground squirrel is more omnivorous than other ground squirrels. A wide variety of pine and fir seeds and nuts, flowers and stems of composites and legumes, foliage of many plant species, fungi, insects, nestling birds, and eggs are eaten. Food preferences shift with local availability; in the autumn when most flowering plants are gone, coniferous seeds make up a high percentage (33%) of the diet. During spring and summer months, golden-mantled ground squirrels are diurnal.

Unlike many other ground squirrels in Montana, the golden-mantled ground squirrel is asocial. The only cohesive unit established in the social structure of this species is between mother and young prior to their dispersal. All other interactions are agonistic and serve to exclude intruders from the area in which the resident individual is active.

Seven to 9 months of the year are spent hibernating, the exact duration influenced by elevation and yearly snow conditions. In Montana, entry into hibernation often begins in late August or early September, slightly later than noted for other ground squirrel species. As winter progresses, torpor bouts increase in length, and animals drop their body temperature to near ambient conditions. Emergence may occur as early as late March at lower elevations; at higher elevations animals may not appear until May.

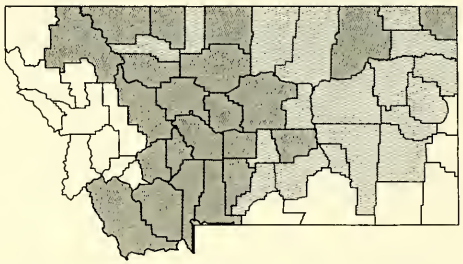
Reproduction: The breeding season of the golden-mantled ground squirrel begins shortly after emergence in spring. Testicular development in males begins several weeks prior to emergence, such that most individuals are capable of breeding immediately on appearing above ground. Reproductive recrudescence of many females lags behind males by a few weeks so that the peak of breeding may not occur until late April or even early May. With a gestation of 27 days, most litters appear by early June. If not bred, or if litters are lost, females will recycle and come into estrus at a later date; litters, particularly from individuals living at higher elevations and emerging later, may appear as late as early August. Litter sizes range between 2 and 8 ($\bar{x} = 5$). Neonates develop rapidly and begin weaning as early as 29 days.

Status: Common.

Bartels, M. A., and D. P. Thompson. *Spermophilus lateralis.* Mammalian Species 440:1–8.

Richardson's Ground Squirrel
Spermophilus richardsonii

Scientific Name: Richardson's ground squirrel was first described, in 1822, by J. Sabine, Secretary of the London Horticultural Society, based on specimens collected by Sir John Richardson at Carlton House, Saskatchewan. Originally identified as *Arctomys richardsonii,* the current usage was first proposed by G. Cuvier in 1831. The generic designation, *Spermophilus,* is derived from the Greek combination sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The specific epithet, *richardsonii,* honors Sir John Richardson, a physician who accompanied Sir John Franklin on 2 expeditions in the early 1800s.



Map 71. Distribution of Richardson's ground squirrel, *Spermophilus richardsonii.*

Description: Richardson's ground squirrel is a somewhat non-descript, medium-sized ground squirrel with pinkish to cinnamon-buff color above and below. Dorsal pelage is slightly shaded with brown tipped hairs. Tail is brown above, intermixed with black hairs tipped with white, and buffy to yellowish below. A light eye ring is apparent. Body length (>275 mm) and hind foot length (>42 mm) are distinguishing external characteristics. Richardson's ground squirrel and the Wyoming ground squirrel can not be distinguished by color alone. Body measurements must be used, although if the animals vocalize, the long, piercing chirp calls of Richardson's ground squirrel are diagnostic as those of the Wyoming ground squirrel are much weaker and shorter in duration. Color of the underside of the tail separates Richardson's ground squirrel from the Uinta ground squirrel, that of the latter being gray. Richardson's ground squirrel lacks the distinct striping or mottling patterns exhibited by all other Montana ground squirrels.

Measurements: [mm(*n*)]: TL = ♂ 319.6(10)/♀ 295.3(10); Ta = ♂ 77.1(10)/♀ 67.9(10); HF = ♂ 45.0(10)/♀ 44.0(10); E = ♂ 12.2(6)/♀ 11.8(9); M [g(*n*)] = ♂ 409.0(3)/♀ 338.9(9). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: Richardson's ground squirrel is a northern species distributed across Alberta, Saskatchewan, and Manitoba southward, dipping into Montana, North and South Dakota, and northwestern Minnesota. It is absent from the western mountainous region of Montana.

Ecology and Behavior: Richardson's ground squirrel was originally abundant across the northern plains. It prefers short grass prairies and pasture land and is capable of inhabiting heavily grazed landscapes. Large colonies develop wherever sandy loam or gravelly soils are available. Burrow systems which lie 1–2 m underground and may extend for over 15 m, are recognized by mounds of dirt thrown up at their entrances. Nest chambers and food storage chambers are within the tunnel system, the former lined with dried grass.

During spring and early summer, above ground activity occurs throughout the day. As the temperature rises during midsummer, activity is bimodal, with peak periods in early morning and evening. Although insects are often eaten, Richardson's ground squirrel is predominantly herbivorous, feeding on a variety of native grasses, such as

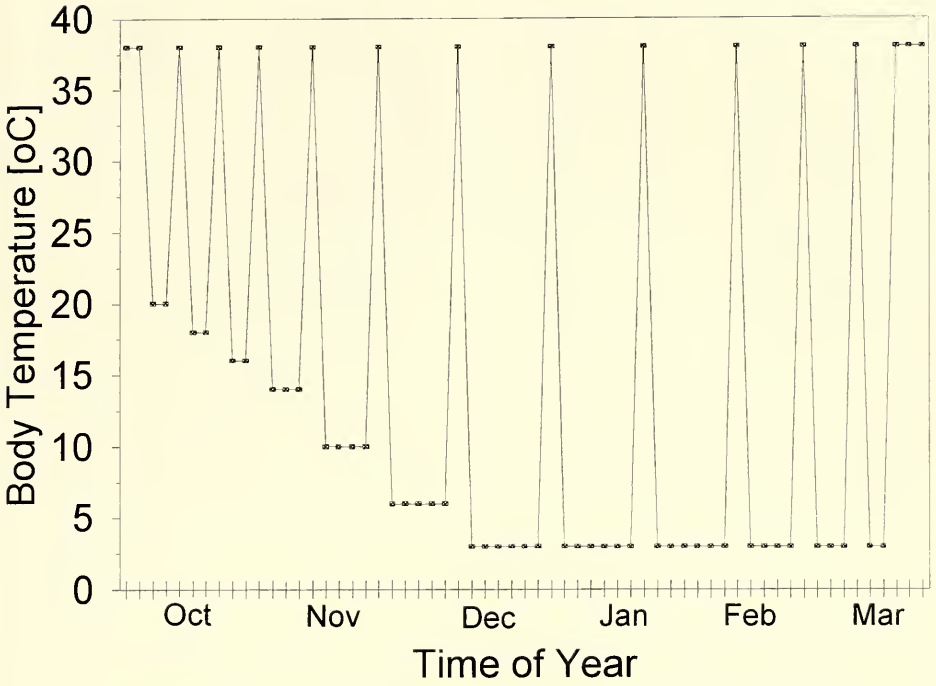


Fig. 58. Time-course of torpor bouts in a winter hibernatory cycle (Wang 1972).

blue grama, pigweed, and locoweed or milk-vetch. It has adapted quickly to commercial agricultural operations, and will feed extensively on grass and legume species which appear on disturbed sites.

Females raise litters independent of males and retain a close association with their offspring. Littermates also recognize and remain close to one another, although are agonistic to non-related individuals. As autumn approaches and animals prepare for hibernation, juvenile males disperse while juvenile females adopt home ranges in close proximity to their natal dens. Such a female dominated social system is described as matrifocal from which matrilines, groups of a female and her female descendants form. Adult males develop and defend territories associated with core areas of several newly emerged females. Such a mating strategy is defined as male defense polygyny.

Emergence of males occurs in early March several weeks prior to that of females. Males, who attain peak breeding condition within 2 weeks after emergence, can mate with 1 or more females quickly after they appear. Although the cue which precipitates the synchronous emergence of males is unknown, females are, in some manner, monitoring and responding to rising soil and air temperatures. With their emergence synchronized to such prevailing environmental conditions, females are able to come above ground just as vegetative growth begins and thus can take maximal advantage of the renewed food source. Unlike emergence from hibernation, entry into hibernation is highly asynchronous and follows the pattern of summer fat deposition established by sex and age cohorts. Adult males, who finish reproduction by the end of April, can turn their attentions to feeding and fat accumulation earlier than adult females or juveniles. Males reach maximal size by late June to early July and immediately begin hibernating. Adult females must contend with pregnancy and lactation, and

can not recover from these energetic costs and renew fat deposition until sometime in June. Thus, females enter hibernation between late July and early August. Adults will nearly double their emergence weight prior to the next period of hibernation. Offspring born in May must grow up before they can deposit adequate stores of fat for hibernation. Females are smaller than males and reach prehibernation weight more rapidly, thus juvenile females hibernate in late August to early September. Juvenile males must continue to grow and deposit fats to reach their requisite prehibernation weight, prolonging their entrance into hibernation until late September or early October.

A classic series of studies on the physiology of hibernation, using this species as the model, demonstrated the stepwise approach taken to lower body temperature over several months, until deep torpor occurs (Fig. 58). By January, torpor bouts last an average of 19 days, interrupted by intertorpor periods of <12 hours. Energetic calculations demonstrated that a >87% energy savings was realized by this behavior.

Reproduction: The breeding season, as indicated above, occurs between mid-March and mid-April, 3–5 days after females emerge from hibernation. Males, having emerged 2 weeks prior, reach peak testicular activity at this time. A single litter is produced each year after a gestation of 22 days. Mean litter sizes at birth are 4.9 (range 3–6) to 8.3 (range of 3–13). Young are weaned by 25 days, growing rapidly prior to emergence in late summer to early autumn. Sexual maturity is reached at 11 months as animals emerge the following spring.

Status: Common and locally abundant.

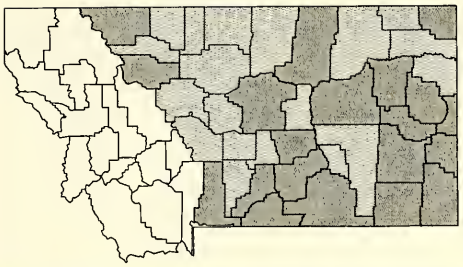
Michener, G. R., and J. W. Koeppl. 1985. *Spermophilus richardsonii.* Mammalian Species 243:1–8.

Thirteen-lined Ground Squirrel
Spermophilus tridecemlineatus

Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*).

Scientific Name: The thirteen-lined ground squirrel was first described by S. L. Mitchill, in 1821, from specimens obtained from central Minnesota. Originally identified as *Sciurus tridecem-lineatus,* this name was changed to the current one, in 1849, by Audubon and Bachman. The generic designation, *Spermophilus,* is from the Greek combination, sperma, which means "seed," and philos, which means "loving;" thus "seed loving." The specific epithet, *tridecemlineatus,* is from the Latin combination, tridecem, which means "thirteen," and lineatus, which means "lined," a reference to the body's striping pattern.

Description: Surely the most distinctive ground squirrel in the state, the thirteen-lined ground squirrel is easily identified by the alternating dark (brown or



Map 72. Distribution of the thirteen-lined ground squirrel, *Spermophilus tridecemlineatus.*

black) and light longitudinal stripes covering its back and sides. Within each of the dark stripes are found regularly spaced square white spots. This striping pattern breaks up the animal's features and provides protection as it forages among short grasses. In general body confirmation, this ground squirrel is small- to medium-sized and slender.

Measurements: [mm(*n*); Smith 1993]: TL = ♂ 276.1(16), MT 236.0(3)/♀ 276.9(16); Ta = ♂ 98.7(15), MT 85.3(3)/♀ 92.1(14); HF = ♂ 37.9(16), MT 31.0(3)/♀ 38.4(15); E = ♂ 8.3(3)/♀ none; M [g(*n*); Smith 1993] = ♂ 162.2(8), MT 143.8(1)/♀ 179.4(6). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The thirteen-lined ground squirrel is found across a large portion of the central United States, from Texas to the Canadian provinces of Manitoba, Saskatchewan, Alberta, and the southeastern most corner of British Columbia. A line from Montana through Wyoming, Utah, and Arizona defines its westernmost boundary; it extends as far east as Ohio, although its southeastern distribution stops at a line running across Missouri, Illinois, and Indiana.

Ecology and Behavior: The thirteen-lined ground squirrel has 1 of the largest distributions of any sciurid inhabiting short grassland prairies. It readily uses disturbed sites such as grazed pastures, and mown grass habitats such as roadsides and even golf courses. Native western short grasslands comprised of grama, needlegrass, and threeawn support populations.

The thirteen-lined ground squirrel has a solitary social structure and the family unit is intact only for a short period after the young emerge. Juveniles disperse within 2 weeks and attempt to establish their own home ranges prior to hibernation. Adults only interact during the breeding season; following breeding agonistic behavior is displayed, as male and female home ranges overlap, although territoriality is not well-defined. Three types of burrows are constructed, each with a different purpose. Nesting burrows are used during the summer to raise a litter. They are typically 2 m or more in length and at least 43 cm in depth; several entrances may service these. The nest cavity is filled with dried grass, and an additional chamber is often used for defecation. Many short, shallow burrows (<1.25 m deep and 23 cm deep) are constructed, primarily as short-term hiding or resting sites. Lastly, deeper burrows are made and inhabited for a majority of the year, as the animals hibernate. Such burrows are much deeper with nest chambers at 64–152 cm depth, well below the average frost depth for the region, and they may extend for 6 m. Such burrows have an earthen plug for added protection.

The thirteen-lined ground squirrel is strictly diurnal. In the spring and early summer before ambient temperatures rise, most activity occurs between 0900 and 1700 hours, peaking at 1200 hours. As summer temperatures increase activity becomes bimodal, with most activity around midmorning and late afternoon. Most time above ground is spent foraging. The thirteen-lined ground squirrel is more omnivorous than others in Montana. A significant percentage of the diet (>50–70% in the spring and late summer) is insects, particularly grasshoppers and lepidopterous larvae. Seeds of grasses (particularly slender fescue and alkali saltgrass), become important as autumn approaches, and the animals prepare to hibernate. Small birds, lizards,

and even young cottontails also may be eaten.

Hibernation consumes a majority of the year. Entrance into hibernation begins in late July to August to late September, although the exact time varies with prevailing environmental conditions and locality. Significant weight gains of 35–40% occur prior to hibernation. As with other obligate hibernators, the thirteen-lined ground squirrel moves into deep torpor gradually during the 1st several weeks. Ultimately, a deep state of torpor is attained with the animal's body temperature held at 1°C–3°C above ambient for >3 weeks at a time. Emergence begins in April, with males preceding females by 1 week.

Reproduction: The breeding season begins shortly after females emerge in the spring. Testicular recrudescence begins in males while they are still hibernating such that they can breed immediately on emergence. Females display estrus within 5 days post-emergence at which time most mate, although breeding activity may span a 2–3 week period. A gestation of 27 days produces most litters in early to mid-May. Mean litter sizes throughout the northwestern portion of distribution range from 6.2–8.7. Young are weaned by 28 days when they emerge from their natal burrows. Sexual maturity is reached at 11 months of age.

Status: Locally common.

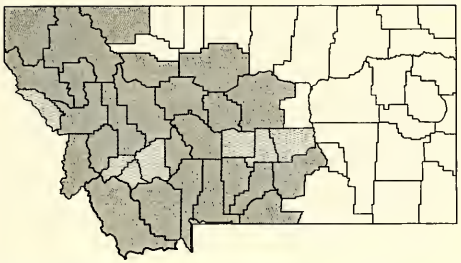
Streubel, D. P., and J. P. Fitzgerald. 1978. *Spermophilus tridecemlineatus.* Mammalian Species 103:1–5.

Yellow-pine Chipmunk
Tamias amoenus

Yellow-pine chipmunk (*Tamias amoenus*). See plate 8.

Scientific Name: The yellow-pine chipmunk was first described by Joel Asaph Allen (1890), a distinguished mammalogist and ornithologist, and curator for both the Harvard Museum of Comparative Zoology and the American Museum of Natural History. His description, published in 1890, was based on specimens from Fort Klamath, Oregon. Although Allen's scientific designation is in use today, the generic distinction was, for many years, *Eutamias.* The current generic designation, *Tamias,* is Greek for "a storer," a reference to this species' food-storing behavior. The specific epithet, *amoenus,* is from the Latin for "pleasing" or "lovely."

Description: The yellow-pine chipmunk is a small chipmunk, only slightly smaller than the sympatric red-tailed chipmunk, both of which, however, are the largest members of the genus in Montana. The yellow-pine chipmunk is characterized by 5 black, longitudinal stripes, separated by 4 light stripes (median stripes are cinnamon; lateral ones are creamy white) which run along its dorsal surface. The 3 dark, midline stripes extend from the shoulder to the rump, the lateral 2 stripes only appear along the middle portion of the body. Body color is a dark red set against cinnamon, with a gray cast. The underside of the tail is a pink- to brown-cinnamon. The yellow-pine chipmunk is 1 of 4 chipmunks in Montana. Where sympatric with the least chipmunk in the southwestern portion of the state, the



Map 73. Distribution of the yellow-pine chipmunk, *Tamias amoenus*.

yellow-pine chipmunk will be the larger, with a proportionately shorter tail, and a more redder hue to its tail (the least chipmunk will be paler and more yellow). Often individual yellow-pine chipmunks within a local population are difficult to distinguish from sympatric red-tailed chipmunks. The latter is most easily identified by its redder shoulder patches and brighter rufous color of the ventral tail surface. In addition the venter of the least chipmunk is more yellow while that of the red-tailed chipmunk in Montana is more gray.

Measurements: [mm(*n*)]: TL = ♂ 205.6(10)/♀ 215.6(10); Ta = ♂ 86.9(10)/♀ 89.5(10); HF = ♂ 26.2(10)/♀ 32.0(10); E = ♂ none/♀ 18.3(4); M [g(*n*)] = ♂ 50.2(10)/♀ 50.8(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The yellow-pine chipmunk ranges from central British Columbia, and the western most edge of Alberta, southward, encompassing Washington, Oregon, Idaho, and western Montana and Wyoming. Further extensions occur into California, Nevada, and Utah.

Ecology and Behavior: Montana's chipmunks can be more readily distinguished by the laymen based on ecological correlates than on anatomical attributes. The yellow-pine chipmunk strongly prefers drier, brushy habitats associated with shrubs, which provide a ready source of food (e.g., buckbrush, snowberry, currant). Natural openings within forested stands of lodgepole pine, ponderosa pine, or Engelmann spruce, or those provided by habitat disturbance (e.g., fires, logging activities), are quickly inhabited. As the forest canopy is opened and the forest floor is carpeted by grasses or shrubs, the yellow-pine chipmunk expands, and competitively excludes the red-tailed chipmunk. The latter species prefers the moist, closed canopy environs of a more mature stand.

Den sites occur underneath logs or stumps, quite often where additional shrub cover is available. Tunnels to the nest cavity may be 2–3 m in length and often 1.5 m deep. Nests are constructed of dried grass. Yellow-pine chipmunk nests also occur above ground in shrubs or trees. One nest in southwestern Montana was in a clump of willows 2.6 m above ground. It was made of dry grass, and measured 15 cm deep by 35 cm wide. Such arboreal nests may provide protection from predators and ready access to seeds and fruits.

As with other species of chipmunk, the yellow-pine chipmunk is omnivorous, feeding on a wide array of plant and animal materials. Seeds from herbaceous and coniferous species make up a high percentage of the diet, as do insects and hypgeous fungi. The yellow-pine chipmunk will collect and dry mushrooms by hanging them under shrubs. Bird's eggs and small vertebrates are also eaten. Foraging is concentrated during early morning just after sunrise as temperatures begin to warm. On the hottest days, activity becomes bimodal or even trimodal with peaks in the early morning and late afternoon and with a short foraging bout at sunset. As autumn approaches, and the animals prepare to hibernate, foraging increases in order to fill food caches.

Unlike ground squirrels, chipmunks can not deposit adequate fat stores to carry them entirely through the winter. Increased foraging in late summer provides animals with greater fat deposits, however much effort is still expended to hoard food for periodic use during the coldest months. Winter food caches can contain 14,000–68,000 seeds and corms weighing 70–190 g. En-

trance into hibernation is highly variable, dependent on prevailing temperatures and food availability. In Montana, individuals disappear in late October to early November and reappear in mid-to-late March. Torpor bouts during this period last from 1 to 2 weeks. Animals which awaken between such bouts may take advantage of their stored foods. As with the ground squirrels, males emerge 1 to 2 weeks prior to females.

Reproduction: Breeding begins shortly after adults emerge in spring, in early to mid-April. Testicular development, initiated during hibernation, allows males to successfully mate within a few days, to a few weeks of emergence. Gestation length is probably 28–31 days as in other members of the genus. Litters average 4–5 young; adult body size is attained by autumn, and sexual maturity is reached the following spring.

Status: Common.

Sutton, D. A. 1992. *Tamias amoenus.* Mammalian Species 390:1–8.

Least Chipmunk
Tamias minimus

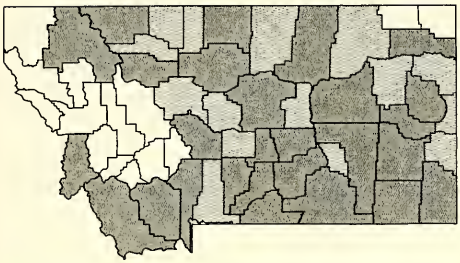
Scientific Name: The least chipmunk was first described by Dr. John Bachman (1839), a close friend of John J. Audubon's and a well respected naturalist in his own right, based on specimens obtained from Green River, in Sweatwater County, Wyoming. Although the generic name was changed, in 1901, to *Eutamias,* the original designation of *Tamias minimus* has returned. The generic designation *Tamias* is from the Greek meaning "a storer;" a reference to the hoarding activities of members of this genus. The specific epithet *minimus* is Latin for "least" or "smallest" and is from which the vernacular name is derived.

Description: As the vernacular name implies, the least chipmunk is among the smallest of chipmunks and definitely the smallest in Montana. Body length is <110 mm and should be diagnostic. In color, the least chipmunk is much paler than others and more gray. Stripes on dorsal and lateral surfaces are less distinct, with only the former being dark black. Venter is grayish-white and the underside of the tail is yellow. Most often the least chipmunk should not be confused with the other 3 species found in Montana. Body color and size are diagnostic. The least chipmunk lacks the red shoulders and tail of the red-tailed chipmunk and the darker striping of both the red-tailed and Uinta chipmunks. The red-tailed and Uinta chipmunks are also considerably larger. Of the 3, the least chipmunk would be most easily confused with the yellow-pine chipmunk, although, again, size differences are noticeable, and the yellow-pine chipmunk has a more buffy colored venter and brighter yellow tail.

Measurements: [mm(*n*)]: TL = ♂ 195.8(10)/♀ 194.8(10); Ta = ♂ 83.3(10)/♀ 85.0(10); HF = ♂ 31.0(10)/♀ 30.7(10); E = ♂ 15.1(9)/♀ 14.7(8); M [g(*n*)] = ♂ 41.5(10)/♀ 46.1(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The least chipmunk is widely distributed across northern and western North America, extending from the Yukon across the Canadian provinces, nudging into Quebec, southward to New Mexico and Arizona. East to west populations extend from the Dakotas, Nebraska, and Colorado, to Washington, Oregon, and the eastern border of California.

Ecology and Behavior: Although the least chipmunk uses a wide range of habitats, from the deserts and sagebrush com-



Map 74. Distribution of the least chipmunk, *Tamias minimus*.

munities of eastern Montana to the alpine tundra of the Beartooth Plateau, it is most prevalent in the alpine tundra. The least chipmunk is the most highly adapted of Montana chipmunks for the more xeric conditions found in the east. Rocky outcroppings are favored for den sites, although burrows may be dug. Natural vegetation, such as denser stands of sagebrush among rocky areas, or overgrown grass along fencerows are used frequently.

Grasses, flowers, and seeds are eaten. Flower heads of sagebrush and seeds of Russian thistle are well liked (Davis 1939). As with other chipmunks, seeds are packed into cheek pouches during a foraging bout and carried back to an underground granary. Activity is diurnal during spring and summer. Short periods of estivation may occur during the hottest summer months, with hibernation beginning in late autumn. Animals emerge as early as February in lower elevation and warmer environs.

The least chipmunk may be the shyest chipmunk, a behavior which is best explained by the areas which it inhabits. Most likely, its secretive nature is a response to the increased vulnerability which the least chipmunk experiences in the more open desert habitats it prefers. Many predators, from a variety of snakes, to skunks, weasels, coyotes, and bobcats, and numerous hawks and owls, effectively hunt them.

Reproduction: Breeding begins shortly after animals emerge from hibernation in spring. For most populations, this occurs in April and May. Pregnant and lactating females, and females with recent placental scars, were captured in early June in South Dakota and Wyoming (Turner 1974). Litter size averaged 4.5 (range 3–6), and a few lactating females were observed as late as August. Gestation is probably 28–31 days.

Status: Locally common.

Red-tailed Chipmunk
Tamias ruficaudus

Red-tailed chipmunk (*Tamias ruficaudus*). See plate 8.

Scientific Name: The red-tailed chipmunk was first described by Arthur H. Howell, a field assistant for the United States Biological Survey, in 1920 based on specimens obtained at upper St. Mary's Lake, in what is now Glacier National Park (Glacier County, Montana). Howell made extensive collections of birds and mammals in Montana in the early 1900s. Originally denoted as *Eutamias ruficaudus*, the current name was first applied, in 1940, by Ellerman. The generic designation, *Tamias*, is Greek for "a storer," a reference to food storage activities. The specific epithet, *rufi-*

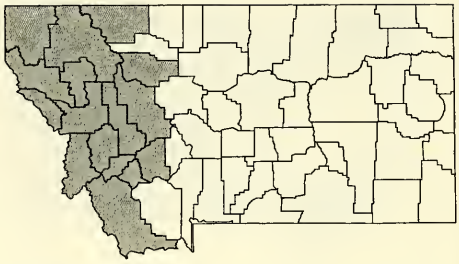
caudus, is derived from the Latin combination, rufus, which means "reddish," and cauda, which means "tail," a diagnostic characteristic for this species.

Description: The red-tailed chipmunk is a medium-sized chipmunk, darkly colored an orange-brown over its dorsal surface, with a grayish-white venter. Its brilliant rufous tail (from which the vernacular name is derived) and cinnamon–brownish head and face are distinctive. Often rufous shoulder patches are noticeable. Black striping along its dorsal and lateral surfaces is sharper and blacker than in other, closely related species, and the alternating lighter stripes are more yellowish-white than white. Where sympatric with other Montana chipmunks, the red-tailed chipmunk is always larger. The darker red tail, and more white ventral body surface, are the most diagnostic characteristics. The yellow-pine chipmunk has a yellower venter and more orange-yellow tinged tail. The red-tailed chipmunk is not sympatric with the Uinta chipmunk. The red-tailed chipmunk is grayer overall with browner striping, and a less rufous tail.

Measurements: [mm(*n*)]: TL = ♂ 216.9(10)/♀ 223.4(10); Ta = ♂ 92.3(10)/♀ 95.4(10); HF = ♂ 32.8(10)/♀ 32.9(10); E = ♂ 16.0(2)/♀ none; M [g(*n*)] = ♂ 56.2(10)/♀ 61.3(10). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The red-tailed chipmunk is relatively narrowly distributed from southeastern British Columbia and the southwestern most corner of Alberta, through eastern Washington, northern Idaho, and western Montana.

Ecology and Behavior: The red-tailed chipmunk is most abundant in dense, subalpine coniferous forest stands, broken by small openings in the canopy which provide a shrub understory for food and cover. In Montana, it occurs in stands of Douglas fir, Englemann spruce, western hemlock, western red cedar, ponderosa pine, western larch, lodgepole pine, and grand fir. Understory components of its habitat have abundant ground and shrub cover.



Map 75. Distribution of the red-tailed chipmunk, *Tamias ruficaudus.*

Where overlapping, the red-tailed and yellow-pine chipmunks are allopatric. The yellow-pine chipmunk prefers the more open forest stands of the ponderosa pine and Douglas fir.

Red-tailed chipmunks are more arboreal than yellow-pine chipmunks and spend considerable time foraging along branches of shrubs and trees. Nests, formed from dried grasses and twigs, are often high in trees placed in notches of branches close to the trunk. In northeastern Washington 3 nests were found 5.8–18.3 m above ground, in Englemann spruce trees. Ground nests are also common and occur at the base of tree stumps, in log piles, and within rock outcrops.

The red-tailed chipmunk is predominantly diurnal, appearing as the sun rises and begins to warm the woods. Foraging may continue sporadically throughout the day. A wide variety of seeds and fruits are eaten. In western Montana (Missoula and Lake counties), seeds of 51 species were collected from cheek pouches. Among these, were the seeds of ponderosa pine, Douglas fir, service berry, snow bush, huckleberry, and buckbrush. Flowers and leaves of arnica, dandelion, and balsamroot are also important. A tell-tale sign of red-tailed chipmunk activity, is the pile of pappus (the modified calyx of composite flowers) left at the base of thistles. Seasonal shifts in diet occur as food availability changes. The red-tailed chipmunk spends much time on the ground, in the spring, taking advantage of

newly emerging seedlings. Foraging shifts to the shrub canopy in summer, as these plants begin to flower and fruit, and in the autumn red-tailed chipmunks move further up into the tree canopy.

Animals disappear below ground in the late autumn (October–mid-November), reappearing in late March to early April. Food caching behavior allows individuals to eat periodically throughout the winter and only a slight gain in overall body weight occurs before hibernation.

Reproduction: In western Montana breeding begins in late April at lower elevations, extending into late May at higher elevations (Beg 1971). Males have scrotal testes, with mature spermatozoa, as early as the 1st week in April. Between 68 and 83% of older females successfully conceive in a given year. Litter sizes range from 4–6 ($\bar{x}$ = 5.16 at lower elevations and 4.54 at higher elevations). Gestation is probably 28–31 days. Parturition extends from late May through late July depending on seasonal conditions and elevation. Young appear above ground at 6 weeks; sexual maturity is reached during the 2nd spring, at 10 months.

Status: Common.

Best, T. L. 1993. *Tamias ruficaudus*. Mammalian Species 452:1–7.

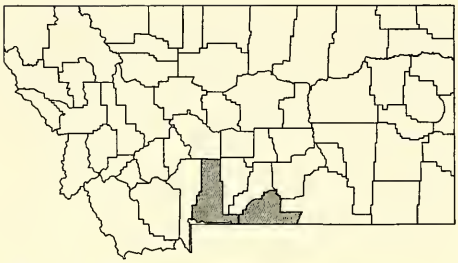
Uinta Chipmunk
Tamias umbrinus

Scientific Name: The Uinta chipmunk was first described by Joel Asaph Allen (1890) from specimens collected at Blacks Fork, in the Uinta Mountains of Utah. Allen was a highly respected mammalogist and ornithologist who served as curator of birds at Harvard Museum of Comparative Zoology, and eventually at the American Museum of Natural History. The generic designation, *Tamias*, is from the Greek, meaning "a storer;" a reference to the genus' active storage of food. The specific epithet, *umbrinus*, is from the New Latin umbrinus, meaning "darkened or shady," a reference to its general body color.

Description: The Uinta chipmunk is a large chipmunk, similar in size and general appearance to the red-tailed chipmunk. The dark stripes along the dorsal surface are broad, more brown-black in color than pure black, and the lighter alternating stripes are more white than gray or yellow. The head, rump, and sides are brown-gray and the venter is white. The Uinta chipmunk can be distinguished from the closely related red-tailed chipmunk by the color of its shoulders and face (gray-brown versus red in the red-tailed chipmunk). Careful notation of the locality will also be diagnostic, as the Uinta chipmunk is not sympatric with the red-tailed chipmunk. The Unita chipmunk, in Montana, is only found in sympatry with the yellow-pine and least chipmunks. It can be distinguished from the yellow-pine chipmunk by color (specifically its white venter) and from least chipmunk by size.

Measurements: [mm(n); 1 Wyoming specimen from border included]: TL = ♂ 227.0(1)/♀ 232.3(3); Ta = ♂ 108.0(1)/♀ 93.0(3); HF = ♂ 32.0(1)/♀ 31.7(3); E = ♂ 19.0(1)/♀ 18.5(2); M [g(n)] = ♂ 55.2(1)/♀ 68.9(2). Dental formula: i 1/1, c 0/0, p 2/1, m 3/3, total 22.

Distribution: The Uinta chipmunk has a disjunct distribution throughout the westcentral United States. Four major regions, with outliers, are inhabited, extending from Montana to Arizona, and California to Colorado. It is at its northernmost limit in southwestern Montana.



Map 76. Distribution of the Uinta chipmunk, *Tamias umbrinus*.

Ecology and Behavior: Probably the Uinta chipmunk is ecologically similar to the red-tailed chipmunk. The Engelmann spruce–subalpine fir forests of Wyoming (Negus and Findley 1959) host the Unita chipmunk and the Uinta chipmunk occurs above timberline in Wyoming and Montana. Further south, in Nevada and Arizona, ponderosa pine forests are preferred.

In Arizona, the Uinta chipmunk will nest in trees and, in this respect, is similar to the red-tailed chipmunk (Hoffmeister 1971).

The Uinta chipmunk probably has similar nutritional requirements as other chipmunks, feeding on a mixture of seeds and green vegetation opportunistically. Insects may play an important dietary role, particularly above treeline.

Hibernation occurs at higher elevations. Although no caching behavior has been described, the Uinta chipmunk may store food and body fats, to carry it through the winter.

Reproduction: Breeding probably begins in late spring, with parturition in early to mid-summer. Lactating females have been taken in early July, in Wyoming, suggesting that conception occurred between mid-May and mid-June. Gestation length and litter sizes are probably within the range observed for other Montana chipmunks.

Status: Locally restricted and not abundant.

Family Zapodidae—Jumping Mice*

Meadow Jumping Mouse
Zapus hudsonius

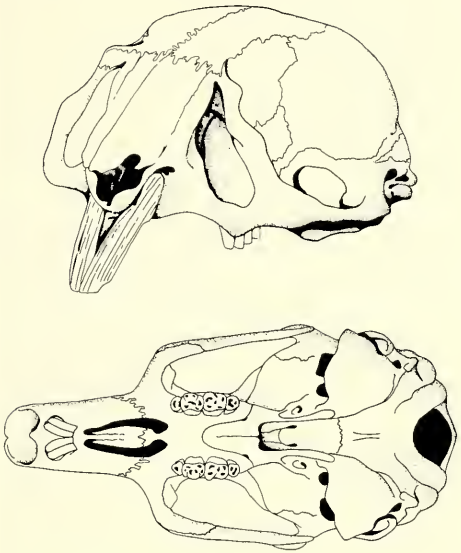


Fig. 59. Skull of a jumping mouse (*Zapus*).

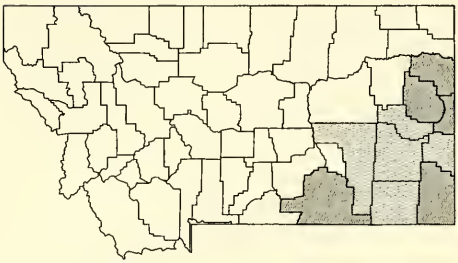
Scientific Name: The meadow jumping mouse was first described by E. A. W. Zimmermann, in 1780, from specimens obtained at Hudson Bay, Canada. Initially designated as *Dipus hudsonius*, Elliott Coues was the first to apply the current name in 1876. The generic distinction, *Zapus*, is derived from the Greek prefix za, which means "very," and the word pus, which means "foot;" a reference to this species extremely large hind feet. The specific epithet, *hudsonius*, identifies the type locality of Hudson Bay from which the meadow jumping mouse was first described.

Description: The meadow jumping mouse, and the closely related western jumping mouse, are 2 of the most colorful and easily identified species in the state. In body form, the meadow jumping mouse is elongate, with a narrow head; well pronounced, nearly naked ears; compact body; markedly large hindfeet; and a long tapering tail. Tail length significantly exceeds body length. The overall color pattern is striking. Along the dorsum, coarse yellowish-brown hair predominates, within which a mid-dorsal darker stripe is produced from black-tipped hairs. The yellowish-brown dorsum is somewhat abruptly offset by yellowish-orange pelage on the sides, and this even more markedly offset by a pure white venter. The tail is bicolored, dark brown above and yellowish-white below. The only species with which the meadow jumping mouse might be confused is the western jumping mouse. The former species is darker in color, with more orange on its sides. The sharply bicolored tail is also diagnostic of the meadow jumping mouse. In overall body size, the western jumping mouse is the larger.

Measurements: [mm(*n*); Smith 1993]: TL = ♂ 209.6(25), MT 222.0(1)/♀ 214.1(15), MT 196.0(3); Ta = ♂ 129.7(25), MT 138.0(1)/♀ 130.7(15), MT 130.5(2); HF = ♂ 30.6(25), MT 27.0(1)/♀ 30.9(15), MT 30.3(3); E = ♂ 15.5(25)/♀ 14.7(15); M [g(*n*); Smith 1993] = ♂ 17.5(25)/♀ 18.6(15). Dental formula: i 1/1, c 0/0, p 1/0, m 3/3, total 18.

Distribution: The meadow jumping mouse is widely distributed from southern Alaska, across the Canadian provinces, to Newfoundland; in the continental United States from the East Coast, as far south as Georgia and Alabama, westward to southeastern Montana, eastern Wyoming, and northcentral Colorado. In Montana, specimens have been collected in Big Horn

* For representative skull characteristics of this taxonomic family refer to Fig. 59.



Map 77. Distribution of the meadow jumping mouse, *Zapus hudsonius.*

County, Carter County (Lampe et al. 1974), and in Wibaux and Richland counties (Matthews 1980; Matthews and Swenson 1982).

Ecology and Behavior: The meadow jumping mouse prefers areas of dense cover in mesic habitats, such as along streams and marshes. It can also be found in forested habitats where significant ground cover abounds. Specimens in Montana have been collected along creek bottoms, woody draws, and grassland coulees, where dense stands of grasses (blue grama; western wheatgrass; needle and thread) and forbs occur (Matthews and Swenson 1982).

The nest is most often constructed from grass which is formed into a ball with a single opening on 1 side. Nests usually occur above ground in dense cover although some individuals may nest under rocks or downed logs, and a few have been observed digging short, shallow burrows. Although most activity occurs during the night, animals may be observed at dawn and dusk, and occasionally during the day. Most activity centers around foraging. The meadow jumping mouse is omnivorous, consuming a wide variety of animal and plant materials. In spring, invertebrates, such as beetles and caterpillars, are favored, but as grasses mature the diet shifts to seeds. The fungus *Endogone* becomes important later in spring and autumn and is selectively sought.

As would be expected from the posture of the meadow jumping mouse, movement through dense vegetation occurs by a short, hopping form of locomotion. The animal progresses in this manner along the ground, using its small front legs to gather grass seeds or dig for fungus. If threatened, individuals may bound up to 1 m at a time, in a similar manner as a kangaroo (referred to as "saltatorial" locomotion). Several jumps will be made before the animal quickly attempts to hide by remaining motionless.

The meadow jumping mouse is solitary in nature, although home ranges may overlap. Little if any agonistic behavior occurs between individuals.

In late August or early September, an increase in seed consumption and a concomitant reduction in basal metabolic rate, allows for a significant weight gain in a span of 1–2 weeks. In the short term, as much as 2 g of weight gain/day can occur at this time, which is nearly 8% of the animal's total body weight (Morrison and Ryser 1962)! When maximum weights are attained, animals enter their hibernation burrows, which are often deeper (up to 0.5 m in depth) than those used during the summer. Hibernation begins in mid-September to early October and extends until late April or early May, a total of over 7 months. As with other true hibernators, this jumping mouse exhibits torpor bouts which, in the coldest months, will last for several weeks. During these periods, with ambient temperatures $\leq 0°C$, core body temperatures will approach 2°C–3°C. As with other hibernatory species, males emerge in the spring, several days before females.

The meadow jumping mouse has high mortality over the winter, particularly among late-litter juveniles. Young, born as a result of the 2nd breeding period in July–August, often can not acquire enough body fat to successfully complete the following hibernation period. Estimates of juvenile mortality range between 75% and nearly 90% (Muchlinski 1988).

Reproduction: Breeding is timed with emergence from hibernation. Males are in breeding condition when they emerge, and

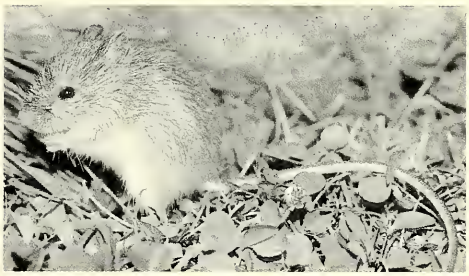
time their exit to precede females. Although 1st matings occur shortly after emergence, most females conceive at least twice during the summer, the 2nd time during a peak in breeding activity between late July and early August. Gestation is 18 days and mean embryo and litter counts are 4.5–5.7 (range 2–9). Of 6 pregnant females collected in Carter County, Montana, the mean embryo count was 6 (Lampe et al. 1974). These animals were collected in July and were at the mid-to-latter stages of gestation.

Development is relatively slow compared to many other small mammals. The external auditory meatus (ear canal) does not open until day 20 and the eyes do not open until day 25. Weaning occurs around the 5th week and full adult body weight is attained at 3 months.

Status: Locally common although not abundant.

Whitaker, J. O., Jr. 1972. *Zapus hudsonius*. Mammalian Species 11:1–7.

Western Jumping Mouse
Zapus princeps



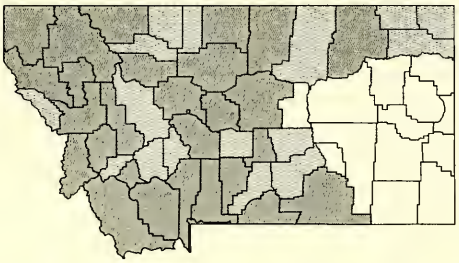
Western jumping mouse (*Zapus princeps*). See plate 8.

Scientific Name: The western jumping mouse was first described by Joel Asaph Allen (1893), from specimens obtained in La Plata County, Colorado. Allen, a curator at Harvard Museum of Comparative Zoology, and later the American Museum of Natural History, collected extensively in Colorado. He was the 1st to produce a list of mammals for Colorado. The generic distinction, *Zapus*, is from the Greek prefix za, which means "very," and the word pus, which means "foot;" this combination refers to this species extremely large hind feet. The specific epithet, *princeps*, is Latin for "first" or "chief;" simply a title given this species because of its unique appearance.

Description: The western jumping mouse is similar to the meadow jumping mouse with which it shares not only body shape but color. In general body form, the western jumping mouse is a medium-sized rodent, with small eyes set in a elongated head, pronounced ears, small forefeet, extremely large hind feet, and a tail longer than its body length. As with the other *Zapus*, body color is distinct. The dorsal surface is marked by a brownish-yellow band which, in the western jumping mouse, is intermixed with whitish or grayish hairs, and is thus paler than in the meadow jumping mouse. Pelage on the sides becomes a more yellowish color and is sharply demarcated from the white venter. Tail is bicolored, although not nearly as sharply as that of the meadow jumping mouse. The only other species in Montana with which the western jumping mouse might be confused is the meadow jumping mouse. The descriptors identified above can be used to distinguish the 2.

Measurements: [mm(*n*)]: TL = ♂ 228.5(10)/♀ 247.2(10); Ta = ♂ 136.3(10)/♀ 148.6(10); HF = ♂ 30.4(10)/♀ 31.0(10); E = ♂ 14.5(7)/♀ 14.7(7); M [g(*n*)] = ♂ 24.2(10)/♀ 27.3(10). Dental formula: i 1/1, c 0/0, p 1/0, m 3/3, total 18.

Distribution: The western jumping mouse is confined to the western portion of



Map 78. Distribution of the western jumping mouse, *Zapus princeps.*

North America, extending from the Yukon, across British Columbia, Alberta, Saskatchewan and into southwestern Manitoba. In the continental United States, it ranges from Washington, Oregon, and California, to the Dakotas, extending as far as New Mexico and Arizona.

Ecology and Behavior: The western jumping mouse is most often found in dense grassy or sedge covered areas, along streams and marshes, although its reliance on such habitats is not as strong as that of the meadow jumping mouse. Such habitats are dominated by alder and willow thickets, and stands of aspen, with sedges and grasses (wheatgrass, bromegrass) as groundcover (Clark 1971; Cranford 1983). More open xeric grasslands in the central portion of the state support the western jumping mouse (predominated by fescue, blue grass, and needle grass—Clark 1971), as do the mesic forests of the west. Populations extend up to higher elevations near timberline, and in some cases can even be found within wet meadows of true alpine habitat.

The western jumping mouse is much more common than the meadow jumping mouse. In certain habitats it may be 1 of the most prevalent of small mammals. Thirty-five individuals were live-trapped over a 2 day period, across 5 ha, in a regenerating stand of Engelmann spruce and subalpine fir northwest of Glacier National Park. Animals have at times been so common that they could be routinely seen while the observer walked through the tall grass. Nests, usually of grass, are similar to the meadow jumping mouse above. Burrows may be dug from beneath logs or dense vegetation.

As with the meadow jumping mouse, the western jumping mouse is omnivorous, relying on a diversity of insect and plant materials opportunistically. Diet shifts throughout the spring and summer reflecting cycles of plant growth (Clark 1971; Cranford 1978). On emergence, animals took advantage of arthropods and green leaves, which accounted for nearly half of the food volume eaten. As vegetative growth reached the flowering stage, flowers were eaten, as were maturing fungi. Toward the end of summer, as grasses and forbs went to seed, they became the dominant food item and accounted for >80% of the diet. Seed consumption is linked to the ability to accumulate fat stores. In laboratory studies, animals fed only seeds had a mean weight gain/day 3 times those fed only green vegetation (Cranford 1978). The high concentration of polyunsaturated fatty acids in seeds is likely responsible for this fat accumulation.

Midway through the summer, 4 weeks prior to hibernation, a dietary shift to seed consumption occurs (Fig. 60), with fat increasing from 20–64% of dry body weight (Cranford 1978). All evidence suggests that animals recognize vegetative changes and are responding to seed availability. The ability to respond to this predictable environmental cue, seed production, prepares the animals for the hibernation period to follow. By consuming seeds as they become available, animals are less affected by unpredictable weather conditions and food resources associated with autumn. A maximum weight of 35 g is attained just before hibernation, at which time the animals begin to lose weight. This weight loss may be associated with final physiological adjustments which are necessary for the pronounced metabolic changes occurring.

Entry into hibernation occurs in early to mid-September for populations living between 2,010–2,900 m in the mountains of northern Utah (Cranford 1978), and 2,600–

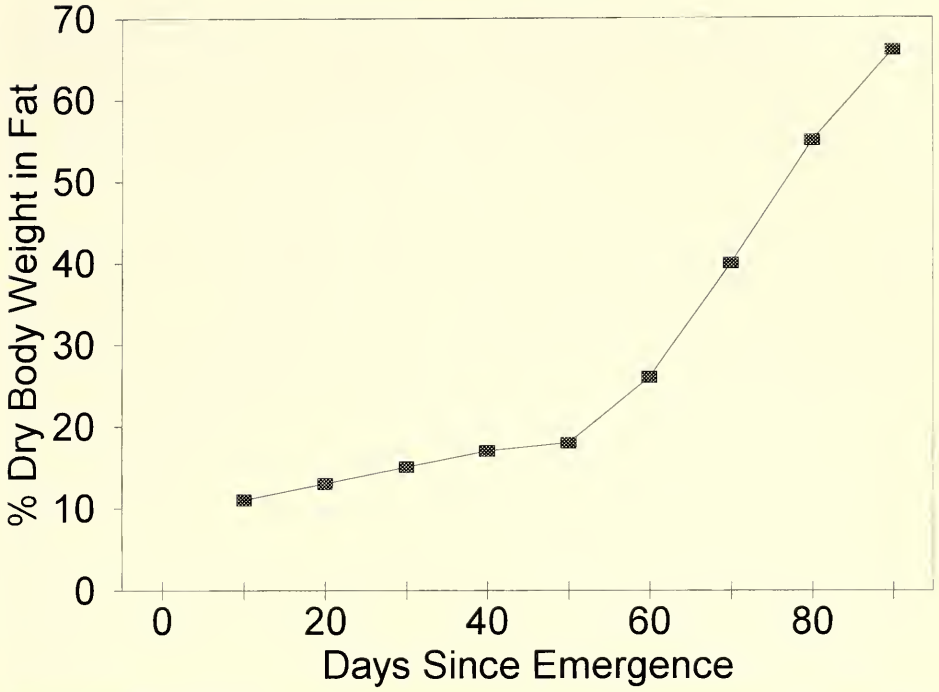


Fig. 60. Percentage of dry body weight in fat in the western jumping mouse as a function of the number of days a population has been active (Cranford 1978).

3,200 m in the mountains of southern Wyoming (Brown 1967a). Animals retreat through a 1–1.3 m tunnel to hibernacula constructed at a depth of 0.6 m. The first 0.5 m of tunnel are plugged with soil, providing additional thermal protection. Periodic torpor bouts occur throughout the colder months. Initially these last for shorter periods of 7–9 days, but as winter progresses extended periods up to 38 days are common (Brown 1967b).

For the western jumping mouse, the cue for termination of hibernation in spring is the gradual increase in soil temperature surrounding the nest cavity (Cranford 1978). Thus western jumping mice can recognize when above ground conditions become favorable. Emergence occurs when the soil temperature reaches 8.5°C–9°C, a temperature which stimulates renewed plant growth. Such conditions occur in Montana in late May to early June. Given this yearly pattern, an average of only 75–120 days (the range depending on elevation—Clark 1971; Cranford 1978) are spent active.

Harsh, prolonged winter conditions can be especially detrimental to juveniles trying to survive their 1st year. Being weaned midway through the summer, these individuals must accumulate adequate fat stores to carry them through winter. Often juveniles enter hibernation at a lower body weight than adults because they have not been able to feed as long. As fats are metabolized during hibernation, body weight decreases and a critical weight of 18–19 g is approached. When this weight is reached, hibernation is terminated regardless of prevailing environmental conditions. An animal reaching this point too early in the spring most often dies. During a normal winter, adult mortality is 25%; juvenile mortality is much higher, ranging from 40–70% depending on conditions (Cranford 1977).

Reproduction: Breeding begins when western jumping mice emerge from hiber-

nation in late spring, late May to early June in Montana. Males emerge with well developed testes, although mature spermatozoa and active spermatogenesis are not seen for an additional 7–12 days (Clark 1971). Peak testicular development occurs 2–4 weeks post emergence (Clark 1971; Cranford 1977). Females emerge 10 days after males, and breeding commences soon thereafter. About 70% of mature females will breed each summer, less than half of the yearling females will become reproductively active (Falk and Millar 1986). Gestation lasts 18 days (Brown 1967b) so that litters of 2–8 ($\bar{x}$ = 4.7–5.4) are born in mid-to-late June (Brown 1967b; Clark 1971; Cranford 1983). Young are weaned by day 25, in late July. Because of the extended period of hibernation and resultant late emergence, only 1 litter is produced/year. Sexual maturity occurs during the 2nd summer at 1 year of age (Brown 1967b).

Status: Common and locally abundant.

ORDER CARNIVORA—CANIDS, FELIDS, MEPHITIDS, MUSTELIDS, PROCYONIDS, AND URSIDS

The order Carnivora is comprised of 240 species organized within 92 genera across 8 taxonomic families, and its members occur on every continent but Antarctica. Their very name, carnivore, conjures up an image of respect, and wonder, and unfortunately fear, as this group of mammals lies at the top of the food chain. The appellation "carnivore" is of Latin derivation, from the combination carnis which means "flesh," and voro which means "to devour." Although some species within this order eat foods other than meat, meat-eating binds them together and focused the evolution of many characteristics from dentition and jaw musculature to predatory behavior.

By their very nature and role in the order of life, carnivores are less abundant than members of other orders and often more secretive. This secretive behavior strengthens their mystique in our minds and makes them even more fascinating.

Carnivores come in a wide range of sizes from the smallest, the least weasel, which weighs in at 70 g, to the largest, the brown ("grizzly") bear, topping the scales in Alaska at over 780 kg. Most species lie at the lower end of this range averaging 2 to 4 kg, although the larger species attract our attention and concern. All members share many unique characteristics (Fig. 61). Key among these is the presence of modified teeth for holding, tearing, and cutting tissue. The teeth are strong and solidly rooted to the jaw bones. All carnivores in Montana have 3 incisors in the upper and lower jaw on each side. These teeth are small and can be used to strip muscle from bone. Directly behind the incisors are large canines, 1 above and 1 below, which puncture and hold prey. Canines can be large and well-developed as in the wolf and bear. Premolars and molars, which in members of other orders grind vegetation, have in most carnivores become modified to shear or cut tissue. The function of these molariform teeth can be best seen in the felids (cats), and to a lesser degree in the canids (dogs) and mustelids (weasels; refer to the description on "carnassial" dentition in Chapter 1). In addition the jaw muscles are reoriented and strengthened such that the jaws can no longer move sideways, but only open and close.

Claws on the digits of each foot (4–5 depending on the species) are well-developed and are retractable in felids. These are used for grasping prey and for tearing tissue apart. Skeletal modifications decrease the rotation capabilities of the limbs and allow many species to walk on their digits (digitigrade locomotion) ultimately increasing their speed. These structural adjustments and enlarged brain allowed the carnivores (and many other mammalian groups) to develop behavioral characteristics for the stalking and killing of prey.

Fifty-seven carnivore species are found in North America north of Mexico and over one-third, 22, exist in Montana. One in 5 mammal species in Montana are carnivores. They span the entire size range from the least weasel to the grizzly bear and provide Montana with a rich diversity of animals. Six of 8 taxonomic families are represented, with 13 genera.

Family Canidae—Canids*

Coyote
Canis latrans

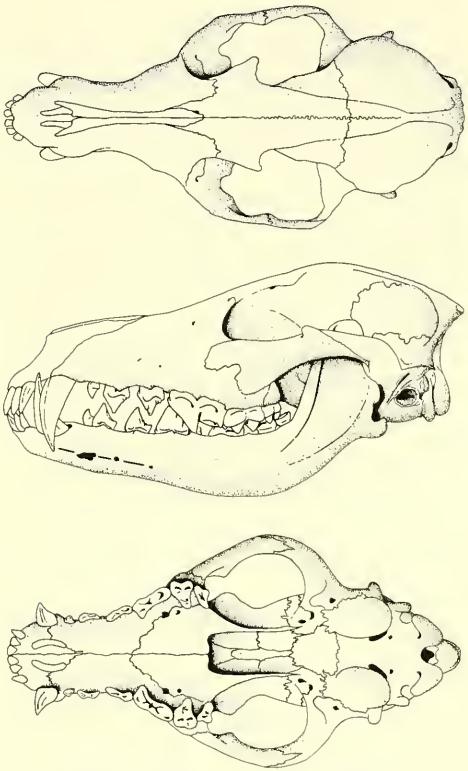


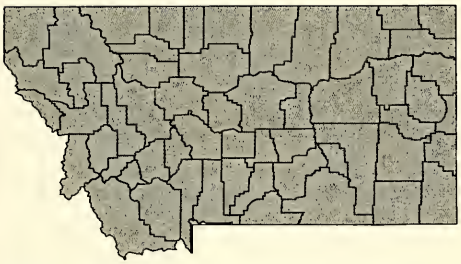
Fig. 61. Skull of a carnivore (*Canis*).

Coyote (*Canis latrans*). See plate 9.

Scientific Name: The coyote was first described by Thomas Say in 1823 from a specimen obtained near Blair, Washington County, Nebraska. At this time, Say was a member of the Long Expedition which traveled extensively through the midwest. However, William Clark, of Lewis and Clark fame, should be credited with identifying the coyote as a new species and bringing it to the attention of the scientific community. The generic designation *Canis* comes from the Latin for "dog." The specific epithet *latrans* is from the Latin meaning "a barker." Thus the coyote was described as a "barking dog." Interestingly, the common name was probably derived from the Aztec word "coyotyl" which also means "barking dog."

Description: The coyote is a medium-sized canid. Although color varies across populations, generally it is grayish-buff to brownish-gray. Very pale individuals have been observed in eastern Montana. Ears are long and a buffy–reddish color on the back. Tail is long and quite bushy, often with a

* For representative skull characteristics of this taxonomic family refer to Fig. 61.



Map 79. Distribution of the coyote, *Canis latrans*.

black patch at its base and always with black tipping. Nose pad is <25 mm in diameter and the footpad is <33 mm. Tracks are generally more elongated than those for most breeds of domestic dog, and the plantar pad on the hind foot is more convex along its leading edge. One interesting behavioral attribute may quickly identify this species from a distance. When running, the coyote carries its tail low, nearly between its legs; domestic dogs and wolves allow the tail to ride up. Because of its close ancestry with the wolf and domestic dog, considerable overlap exists in many physical characteristics. Nose and footpad measurement can distinguish the coyote from the wolf. Several measurements of the skull and teeth also may be helpful in differentiating these species from one another, and from domestic breeds (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 1220.4(5)/♀ 1130.5(2); Ta = ♂ 346.9(5)/♀ 355.8(2); HF = ♂ 147.1(5)/♀ 185.7(2); E = ♂ 111.4(4)/♀ 98.3(2); M [kg(*n*)] = ♂ 12.9(10)/♀ 10.0(2). Dental formula: i 3/3, c 1/1, p 4/4, m 2/3, total 42.

Distribution: The coyote probably originated in the southwestern region of the United States. More recently, over the past 200 years, the coyote has expanded its range to a remarkable degree. It may now be found throughout much of North America as far south as Costa Rica.

Ecology and Behavior: The 1st recorded descriptions of the coyote, provided by William Clark on 18 September 1804 (Moulton 1987a:86) and Meriwether Lewis on 5 May 1805 (Moulton 1987b:112), are illuminating in their detail and provide insight into the original ecology of the species. Both passages are excerpted here:

> Clark: "I Killed a prarie wolf to day about the Sise of a Gray fox with a bushey tail the head and ears like a Fox wolf, and barks liks a Small Dog— The annimale which we have taken for the Fox is this wolf, we have seen no Foxes."

> Lewis: "Capt. Clark found a den of young wolves in the course of his walk today and also saw a great number of those anamals; they are very abundant in this quarter, and are of two species the small woolf or burrowing dog of the praries are the inhabitants almost invariably of the open plains; they usually asociate in bands of ten or twelve sometimes more and burrow near some pass or place much frequented by game; not being able alone to take a deer or goat they are rarely ever found alone but hunt in bands; they frequently watch and seize their prey near their burrows; in these burrows they raise their young and to them they also resort when pursued; when a person approaches them they frequently bark, their note being precisely that of the small dog. they are of an intermediate size between that of the fox and dog, very active fleet and delicately formed; the ⟨years⟩ ears large erect and pointed the head long and pointed more like that of the fox; tale long ⟨and bushey⟩; the hair and fur also resembles the fox tho" is much coarser and inferior. they are of a pale redish brown color. the eyr of a deep sea green colour small and piercieng. their tallons are reather longer than those of the ordinary wolf. . . ."

As Lewis and Clark indicated, the coyote was originally a denizen of the open plains, adapted to these more arid conditions where they fed on small rodents. Even today, with its greatly expanded range, the coyote is still closely associated with more

open habitats, grasslands, and brushy draws. Where the gray wolf has been extirpated, the coyote has flourished. Coyotes tolerate human activity well and appear to be particularly adept at taking advantage of habitat disturbances, such as logging operations and clearing of lands for agriculture. Den sites are often located in cutbanks, in brushy ravines, or under large deadfall. They have more than 1 opening leading into a tunnel which may extend for up to 6 m.

The coyote has an extremely varied diet of innumerable plant and animal materials. It is an opportunistic forager taking advantage of what ever is available, on any given day, in any given season. Meat, of course, is at the core of its diet; most small mammals from rabbits and hares, to numerous rodents such as ground squirrels, mice, and voles are taken. Snowshoe hares and Colombian ground squirrels, in particular, occur in a high percentage of scats analyzed from northwestern Montana (Boyd 1982; Murie 1945), while mountain cottontails, and to a lesser degree white-tailed jackrabbits, occurred in scats from west of Fort Peck, along the Missouri River (Murie 1945). Upland game and song birds, and their eggs, are eaten, as are a variety of amphibians and reptiles. Insects are eaten extensively in the summer and various fruits are consumed as they ripen in late summer or autumn. In winter, carrion may become an important staple, and in early spring newborn deer, elk, bighorn sheep, and pronghorns are taken. Predation on domestic calves and sheep may be a significant problem in some regions of the state. However, finding a coyote feeding on a newborn lamb in spring does not necessarily mean the coyote was responsible for its death. Natural mortality in lambs is high in spring, a result of starvation, disease, and infection, and the coyote is an efficient scavenger. Coyotes also follow wolf packs to scavenge on elk and moose carcasses. This is risky as wolves are often intolerant of coyotes.

Coyotes have an unusual association with badgers (Minta et al. 1992). As badgers enter ground squirrel burrows in search of spring litters, coyotes wait by secondary entrances for emerging animals. Coyotes hunting in this manner increased their capture rate by 34% over individuals hunting alone. Such behavior was documented in Native American folklore (Ramsay 1977).

Coyotes are active year-round; during summer they may be active more frequently during the day, although most activity is centered around dusk and dawn, and throughout the night. Length of movements is influenced by game abundance. Coyotes are constantly on the go. Individuals may cover over 4 km/day, dispersing individuals move >42 km. Most often, coyotes are alone, although during the breeding season and while litters are being raised male–female pairs occur. Males remain with the female while young are nursed and bring food for both the adult female and pups. Coyotes do not have the elaborate social structure that wolves do but juveniles remain with adults to form a den pack. Recent observations in Yellowstone Park, however, suggest that coyote pack behavior exists and that groups of up to 6 individuals may associate. Aggregations of coyotes occurs more often in winter when such behavior may serve as a defensive strategy to protect carrion (Gese and Grothe 1995). Although they may share an area with foxes and bobcats, coyotes are generally intolerant of these competitors. In such areas of Montana where the coyote has been heavily harvested, red fox numbers increased. When pelt prices are low and harvesting pressures are reduced, coyote populations rise and the red fox is forced out. In contrast, mountain lions and wolves do not tolerate coyotes and frequently kill those that they come upon.

Coyotes have a large repertoire of vocalizations with as many as 11 graded signals. Howling occurs at dusk and is the most distinctive vocalization which occurs. Coyote communication is similar to that of jackals; both species raise their heads while howling.

Reproduction: Breeding extends from January through March and is influenced by

latitude (Boyd 1982). Montana breeding begins in late February, and most females conceive within 1 month. Females mate once/season during a 2–5 day period of estrus. Gestation is 63 days (range 58–65). Mean litter size ranges from 4.3–6.9 depending on food availability and population density. Young, blind and helpless at birth, are weaned at 5 to 7 weeks of age. They leave the den and begin exploring their surroundings by 3 weeks of age. Sexual maturity is reached by both sexes as yearlings.

Status: Common. In Montana, the coyote may be killed without a permit. From 1986 to 1995 an average of 8,000 coyotes/year were harvested statewide.

Bekoff, M. 1977. *Canis latrans.* Mammalian Species 79: 1–9.

Gray Wolf
Canis lupus

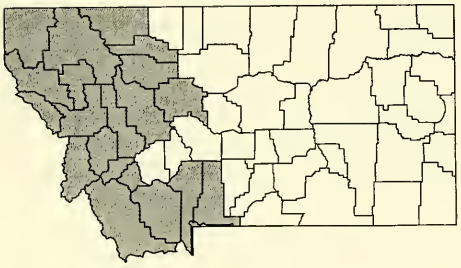
Gray wolf (*Canis lupus*). See plate 9.

Scientific Name: The gray wolf was first described by Carolus Linnaeus, in 1758, from specimens collected in Sweden. The 1st description of the gray wolf in North America was provided by Schreber, in 1775, from specimens obtained in Quebec, Canada. The generic designation *Canis* is Latin for "dog." The specific epithet *lupus* is also Latin and means "wolf."

Description: The gray wolf is the largest wild canid. In color, it is most often a grizzled gray with black guard hairs in abundance mid-dorsally and on the tail and the backs of the ears. Color morphs, from pure white to pure black, are common, with brown shades in between. In general appearance, it closely resembles the common German shepherd or Alaskan malamute. It can be distinguished from the coyote by its overall larger body size, larger skull, width of canines, and other dental differences (Foresman 2001).

Measurements: [cm(*n*); D. Boyd, pers. comm.]: TL = ♂ 186.0(8)/♀ 180.1(10); Ta = ♂ 49.6(7)/♀ 49.6(10); HF = ♂/♀ none; E = ♂/♀ none; M [kg(*n*); D. Boyd, pers. comm.] = ♂ 46.9(9)/♀ 35.5(10). Dental formula: i 3/3, c 1/1, p 4/4, 2/3, total 42.

Distribution: In North America, the gray wolf ranges from Alaska across the Northwest Territories and the western rim of Greenland, throughout the Canadian provinces, with extensions into Idaho, Montana, the northern Great Lakes region, and remote parts of the southwest and Mexico. Several packs have formed in Montana since 1982 primarily from Canadian dispersers. Animals are observed more and more often throughout western portions of the state, particularly along the east front of the Rocky Mountains near Augusta and Choteau, and from Glacier to Yellowstone National parks where they were released in 1995. About 63 gray wolves are now thought to reside in the state, with an additional 118+ in the greater Yellowstone region and 141+ in the central Idaho region, many of whom may cross into Montana pe-



Map 80. Distribution of the gray wolf, *Canis lupus*.

riodically (Unites States Fish and Wildlife Service 1999).

Ecology and Behavior: Historically, gray wolves occurred throughout Europe, most of Asia, and North America as far south as central Mexico. With such a large range, they were found in a variety of habitats from grasslands to dense forest, from semi-deserts to arctic tundra, wherever sufficient prey could be found. During Lewis and Clark's historic expedition (1804–1806) from St. Louis to the Pacific Ocean, wolves were encountered numerous times. First observed on 30 May 1804 near Leavenworth, Kansas, they were frequently observed following large herds of buffalo and killing weaklings that fell behind. Often 10 or more individuals were observed in a day, and many were hunted.

Wolves are best adapted physically and socially to prey on large mammals, particularly ungulates such as deer, elk, moose, caribou, mountain sheep, mountain goats, and bison. Hunting is usually confined to family groups consisting of a pack of 5 to 8 members. A social hierarchy develops as the pack is formed from an adult male and female pairing. The adult male is dominant to the female, and she in turn is dominant to any pups that result. As the pups mature they will become active members of the pack.

Between Glacier National Park and Canada the home range of the founding "Magic Pack" was estimated at 1,795 km^2 from 1985 through 1987 (Ream et al. 1991). Other wolf packs in this region between 1987 and 1988 had home ranges from 343–1,087 km^2. In Alaska daily movements up to 72 km are not unusual. Packs in Montana have a yearly home range and do not migrate. Those in Alaska and the Northwest Territories may migrate with caribou herds covering over 160 km from summer to winter ranges. While foraging, wolf packs appear to be constantly on the move. Estimates for the kill rate of a pack, and thus for the amount of food required to support a wolf, range from 1 deer/wolf/18 days to 1 moose/wolf/45 days. This translates to between 2.5 and 6.5 kg of meat/animal/day.

Reproduction: Breeding extends from January to April depending on latitude. In Montana, most breeding occurs in late winter. Females have a 5–7 day estrus. Monogamy is usual although polygamous mating may occur in some packs. Gestation lasts 63 days and an average of 6 young (range 1–11) are produced. Colonizing wolves in Montana produced litters of 1–9 (Pletscher et al. 1997). The female attends the pups for 2 months during which she and the litter are supplied with food by the male and other pack members. Young are weaned at 5 weeks of age. Pups are moved from the natal den site after 2 months and possibly several times thereafter until they are mature enough to join the pack, often as early as October. At this point they are nearly adult size. Sexual maturity is reached by 2, but breeding often is delayed until 3 years of age.

Status: Populations are increasing throughout western Montana. More than 63 individuals now reside in the state with additional immigration from Canada probably occurring continually. Recent reintroduction efforts in Idaho and Wyoming (Yellowstone National Park) have provided additional animals. The gray wolf was listed as endangered in Montana in 1973 under the Endangered Species Act.

Mech, L. D. 1974. *Canis lupus*. Mammalian Species 37: 1–6.

Swift Fox
Vulpes velox

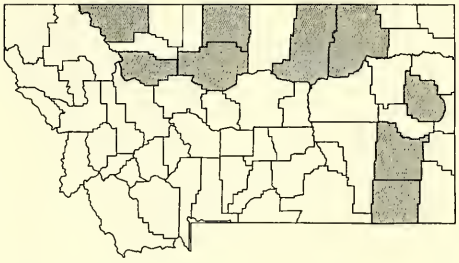
Scientific Name: The swift fox was first described by Thomas Say, in 1823, from specimens obtained along the South Platte River, Colorado. Say may or may not have previously read Meriwether Lewis' journal accounts of the swift fox, dated from July 6th and 8th, 1805; these are the 1st scientific reports known for the swift fox. Originally identified as *Canis velox,* the currently accepted name was applied by Audubon and Bachman in 1851. The generic designation *Vulpes* is Latin for "fox." The specific epithet *velox* is Latin for "swift or speedy."

Although questions have been raised recently about the distinction between the swift and kit foxes, mitochondrial DNA indicates the 2 are separate species (Mercure et al. 1993).

Description: The swift fox is the smallest native canid found in North America. In color, it varies from a dark buffy-gray dorsally with orange-tan sides and legs, and light tan to white venter in winter, to a more reddish-gray summer pelage. The noticeably bushy tail is buffy-gray above and white below, with a black tip. A distinctive blackish-brown spot occurs on each side of the snout. Condylobasal length is <120 mm and a distinctive "U"-shaped temporal ridge exists. As the smallest native canid in the state, the swift fox should not be confused easily with any other species. It is less than one-fifth the size of the coyote. Color and skull characteristics clearly distinguish this fox from the other Montana species, the red fox (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 787.9(19)/♀ 776.0(14); Ta = ♂ 264.2(19)/♀ 274.5(14); HF = ♂ 129.2(19)/♀ 122.2(14); E = ♂ 62.4(19)/♀ 63.5(14); M [kg(*n*)] = ♂ 2.4/♀ 2.3(14). Dental formula: i 3/3, c 1/1, p 4/4, m 2/3, total 42.

Distribution: The historical distribution of the swift fox extended from southern portions of Alberta to central Texas, and from the eastern edge of North and South Dakota, and Nebraska to central Wyoming, Colorado and the eastern portion of New Mexico. Many of these populations are now extinct, thus the current status in many localities is in question. Historical records from Montana dating from the late 1880s placed the swift fox in Glacier (formerly Teton) County. Bailey and Bailey (1918) recorded this species along the plains, on the eastern side of Glacier National Park, although, without further reports for over 50 years, Hoffmann et al. (1969) concluded that it had probably gone extinct in the state. In 1978, a single male was captured in Custer County (Moore and Martin 1980), and since this time several additional specimens have been collected or reliably observed. Sporadic reports have come from Dawson, Hill, Powder River, and Valley counties, and other unconfirmed reports have been made. A reintroduction program initiated by the Canadian Wildlife Service in 1983, and continued through 1991, may be responsible for many of the new sightings in the northcentral region. A total of 284 animals were released during this period in southeastern Alberta and southwestern Saskatchewan. A previous reintroduction in South Dakota in 1980 also may have provided a nucleus for Montana individuals. In August of 1998, 30 swift foxes were reintroduced by the Blackfeet Nation on the Blackfeet Indian Reservation (Glacier County) and an additional 15 animals were released in August of 1999. Additional releases are planned. Stock for these reintroductions have come from Cochrane Ecological Institute, a Canadian organization which maintains the world's only captive breeding facility for the swift fox.



Map 81. Distribution of the swift fox, *Vulpes velox.*

Ecology and Behavior: When Meriwether Lewis first observed the swift fox on 6 July 1805 he was quite impressed:

> "There is a remarkable small fox which ascociate in large communities and burrow in the praries something like the small wolf (coyote) but we have not as yet been able to obtain one of them; they are extremely watchfull and take reffuge in their burrows which are very deep; we have seen them now where except near these falls (the Great Falls of the Missouri, in present day Great Falls, Montana)." (Moulton 1987b:364)

Two days later on 8 July Lewis provided a more detailed description saying:

> "they are very delicately formed, exceedingly fleet, and not as large as the common domestic cat. their tallons appear longer than any species of fox I ever saw and seem therefore prepared more amply by nature for the purpose of burrowing." (Moulton 1987b:367).

As always, Lewis was remarkably perceptive recognizing not only that this was a new species unknown to science at the time, but that it was an adept burrower closely tied ecologically to the prairies.

No other North American canid is as strongly subterranean. Elaborate dens are constructed with up to 9 entrances, and a tunnel system often >1 m in depth and ≥1 m in length. One report describes a tunnel over 4.6 m long, although most are shorter. Entrances are 20 cm in diameter suggesting that the swift fox does not take over abandoned badger or coyote dens. Dens are often clustered together in groups of 3 to as many as 13. They are used throughout the year, may be maintained by an individual for extended periods of time, and are often further modified by successive generations. Exposed sites on hill tops and slopes in cultivated fields or short-grass prairies are preferred, although heavily grazed sites devoid of shrubs are also used. Dominant vegetation is buffalo grass and blue grama, and cultivated fields of winter wheat and alfalfa.

The diet consists of small mammals, birds, reptiles, and invertebrates heavily weighted toward small mammals. Analyses of stomach contents identified lagomorphs, such as the black-tailed jackrabbit and cottontail most frequently in stomachs. Deer mice, harvest mice, and pocket mice were also significantly represented, as were songbirds and quail. Most activity is nocturnal, although during cold periods swift foxes are active at midday sunning themselves at the den entrance.

The decline of the swift fox has multiple causes: extermination programs oriented toward coyotes (and earlier, wolves) using indiscriminate poison bait sets, heavy trapping pressure in the 1800s, loss of habitat with human westward expansion, and coyote–swift fox incompatibility. Recent changes in coyote control programs, and return of the land to native habitat with the decline of homesteads and small ranches, may be responsible for the observed increases. Swift fox probably survived in isolated pockets in many parts of its historical range.

Reproduction: The breeding season extends from late December or early January, through early March in Montana. After a gestation of 50–52 days, litters are born in late March to early May; births in Montana would likely occur at 52 days. Mean litter sizes range from 3.6–4.8 (based on young observed at the den). Litters from captive animals are of 2–7 young. Weaning occurs at 6–7 weeks of age, and adult body size is reached by August. Sexual maturity is attained the 1st breeding season following

birth. Adults mate for life and males participate in rearing young.

Status: Extremely rare. The swift fox is just now making a comeback as a result of reintroductions in Canada, Montana, and South Dakota.

Egoscue, H. J. 1979. *Vulpes velox.* Mammalian Species 122:1–5.

Red Fox
Vulpes vulpes

Red fox (*Vulpes vulpes*). See plate 9.

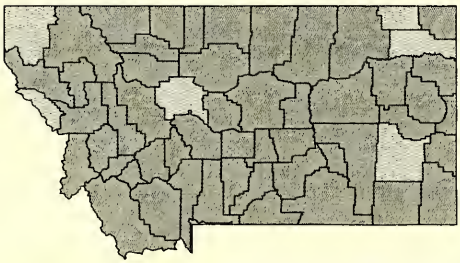
Scientific Name: The red fox was first described from specimens obtained in Sweden by Carolus Linnaeus in 1758 who applied the name *Canis vulpes.* The presence of the red fox in New England, Pennsylvania, and Virginia in the late 1700s may derive from introductions which occurred in the 1750s from Europe. In 1821, the generic distinction was changed to *Vulpes* providing the current name, *Vulpes vulpes.* This name is derived from the Latin word for "fox." It also means "cunning."

Description: The red fox has a distinctive color pattern; dorsal pelage is reddish-yellow (from which the vernacular name is derived), blending into a grayish to white venter. It has a bushy tail which is tipped in white, and its feet, nose, and the backs of its ears are black. Several color variants occur in the wild, the 2 most common being the "silver fox" and the "cross fox." The former is nearly black in color, with white-tipping of its guard hairs providing a silver appearance. Cross foxes are identified by a cross of brown hairs over their shoulders, which continues down the midline. The distinctive white-tipped tail is present on all variants. Because of its distinctive color pattern, no confusion should occur in the identification of red fox. The only other fox in Montana, the swift fox, is significantly smaller in all respects and has a black-tipped tail. Skull size, shape, and appearance are diagnostic with respect to other Montana species (Foresman 2001).

Measurements: [mm(n)]: TL = ♂ 1070.0(4)/♀ 1057.3(3); Ta = ♂ 431.5(4)/♀ 420.0(3); HF = ♂ 185.5(2)/♀ 164.7(3); E = ♂ 101.3(3)/♀ 97.0(3); M [kg(n)] = ♂ 5.5(5)/♀ 4.7(4). Dental formula: i 3/3, c 1/1, p 4/4, m 2/3, total 42.

Distribution: Red fox populations can be found from Alaska and all Canadian Provinces southward, including all the continental United States. Hoffmann et al. (1969) described the expansion of this species from both eastern and western regions of Montana toward the middle, but were unable to provide any evidence of its existence at that time in a band running from Liberty and Hill counties, southeastward through Big Horn County. Harvest records for the 1995–1996 trapping period indicate that a number of animals were taken throughout this region, thus this species probably inhabits the entire state.

Ecology and Behavior: The red fox is adapted to a wide variety of habitats from open grasslands to dense forests. It is most abundant along forest edges and riparian zones. Disturbed areas close to human habitation are frequently used, red foxes may



Map 82. Distribution of the red fox, *Vulpes vulpes*.

Fig. 62. Curious red fox pups.

den in old fields adjacent to new housing developments or adjacent to golf courses. Dens are used only during the breeding season. These may be abandoned badger or skunk dens that are modified, or dens may be dug by the fox itself. Dens occur under abandoned buildings, barns, or haystacks or on a ridge or bank that affords a wide view of the surrounding area. Elaborate burrows may be constructed with multiple entrances (2 to as many as 27 each, 3–6 cm in diameter) and tunnels as long as 70 m (Dekker 1983; Schwartz and Schwartz 1959). Although most burrow systems are probably only a few meters in length, they may contain a grass lined chamber for the young and additional chambers for food storage.

As with the swift fox, rabbits and hares play a dominant role in the diet. Small rodents (e.g., voles, deer mice, pocket gophers, jumping mice, muskrats) are also taken, as are song birds, grouse, pheasants, insects, and some plant materials. Their foraging strategy is to trot over their home range until they pick up the scent of a prey item and then sneak up and pounce on it. Stealth rather than an active chase is the rule. Cooperative hunting between 2 individuals occurs often. Patches of vegetation will be "worked," and 2 foxes may flush prey out of culverts, with 1 animal crawling through while the other waits at the opposite opening. Most activity occurs in the early morning and evening or at night, although animals may be seen infrequently during the day. Outside the breeding season, foxes will simply curl up beneath deadfall or brush, or even in the open to rest rather than use a den.

Where the red fox is in sympatry with the coyote, it is often harassed, if not outright preyed upon. Populations of these 2 species are often found in an inverse relationship, primarily in response to avoidance of the coyote by the fox. Similar relationships occur between wolves and coyotes, and between mountain lions and coyotes, with coyotes being preyed on. As mentioned above, populations of the red fox were thought to have been augmented by importations from Europe in the mid-1700s, for sport hunting. Depending on pelt prices, which fluctuate yearly, the red fox is still sought for its luxuriant winter fur.

Reproduction: Breeding occurs during January and February in this region. Female receptivity (heat) lasts only 1–6 days. One litter/year is produced between March and April after a gestation of 53 days. Litter sizes average 4–6. As with coyotes, pups may be moved more than once between dens during the first 2 months (Fig. 62). The male cooperates in raising the young by bringing food to both the nursing female and developing pups. At 2 months of age,

young are weaned and will begin to travel with adults on foraging bouts. Adult weights are nearly attained by autumn at which time the young disperse. Sexual maturity for both males and females is reached during the 1st winter, although the number of individuals breeding at this age varies with locality.

Status: Common and increasingly abundant. Although trapped heavily for its fur, it is classified as a nongame species. Since 1990, between 4,000 and 11,000 animals/year were legally harvested, a majority from the southcentral and southeastern regions.

Lariviere, S., and M. Pasitschniak-Arts 1996. *Vulpes vulpes*. Mammalian Species 537:1–11.

Family Felidae—Felids*

Mountain Lion
Puma concolor

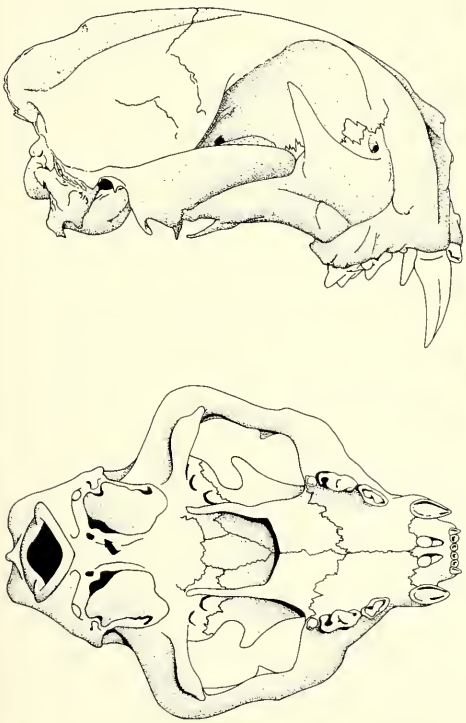


Fig. 63. Skull of cats: *Puma*, top; *Lynx*, bottom.

Mountain lion (*Puma concolor*). See plate 10.

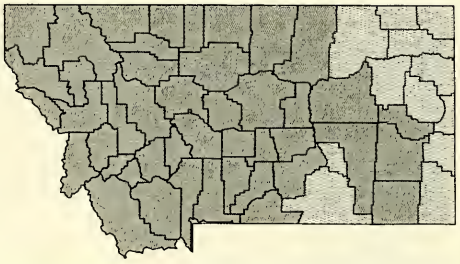
* For representative skull characteristics of this taxonomic family refer to Fig. 63.

Scientific Name: The mountain lion was first described by Carolus Linneaus in 1771, from specimens obtained in Cayenne, French Guiana. The 1st description in North America was provided by Kerr, in 1792, based on specimens from the Carolinas, Georgia, and Pennsylvania. Although the generic name for this species is currently in question I have retained the classification accepted by Jones et al. (1997). The generic designation *Puma* is Peruvian, a name applied to their native cat. The specific epithet *concolor* is a combination of 2 Latin words, con which means "together," and color which means "color;" a reference to the consistent color over its body.

Description: The mountain lion, also known as the puma, cougar, or panther, is the largest felid in North America reaching a total length >2.2 m. It has a robust, cylindrical tail nearly one-third its total length and short, rounded ears. As a felid it has retractile claws. Dorsal pelage varies from a pale grayish-brown to more buffy, or even darker reddish-brown. The venter is creamy-white. A distinctly darker brown to black color exists on the lateral muzzle, backs of ears, and tip of tail. Other Montana felids, the bobcat and lynx, are considerably smaller and markedly different in color and body features.

Measurements: [cm(*n*); Smith 1993]: TL = ♂ 217.0(11)/♀ 194.0(36); Ta = ♂ 79.0(12)/♀ 71.0(36); HF = ♂ 27.6(4)/♀ none; E = ♂/♀ none; M [kg(*n*); Smith 1993] = ♂ 71.0(11)/♀ 44.0(34). Dental formula: i 3/3, c 1/1, p 3/2, m 1/1, total 30.

Distribution: The historical distribution of the mountain lion extended from British Columbia throughout the continental United States to Chile and Argentina. Significant habitat alterations over the past 200 years, as the United States grew, and associated control measures targeting the mountain lion, have greatly reduced its range. Presently, most populations exist in the western United States, inhabiting more mountainous regions where seclusion is still possible. Isolated pockets occur across the country.



Map 83. Distribution of the mountain lion, *Puma concolor.*

Ecology and Behavior: Coupled with a foraging strategy that uses stealth and heavy persecution by humans, the mountain lion is mostly restricted to more wooded, western habitats. As 1 of the largest predators in North America, the mountain lion relies heavily on larger prey species such as mule deer, white-tailed deer, and elk. Activity may occur throughout the 24-hour period. Increased daytime activity occurs in association with hunting of Columbian ground squirrels. Elk and deer kills during winter months occur in evening, nighttime, and mid-morning hours. Older elk and deer, particularly males, and young individuals are most vulnerable. Selection appears to be for weaker animals. About 1 deer/10–14 days is needed to sustain an adult lion during winter. Such predation pressure does not significantly impact elk and deer populations. Following a successful hunt, the lion will gorge itself and then retire to rest. The carcass is covered with leaves and dirt and revisited within a few days. Three lions, a mother and 2 adult-sized yearlings, ate an entire mule deer in 2 days, leaving only a small pile of perfectly cleaned bones, and the stomach contents as evidence of their kill. Mountain lions are 1 of the main predators of porcupines, avoiding its defensive quills by flipping the animal on its back and attacking the vulnerable belly. As with most predators, when preferred prey are not available, it will oppor-

tunistically take whatever is available including small mammals, birds, fish, and insects. Domestic livestock are also taken occasionally.

No permanent den site is constructed nor used. Mountain lions continually move throughout the year over their home range, stopping to rest under rock ledges or piled deadfall. Maternity den sites are chosen for the protection which they afford and are often found in dense, brushy areas, particularly under large deadfall. This species is solitary, with males and females adopting separate home ranges. Those of adult males do not overlap, although those of females may overlap other females or possibly an adult male. Home range sizes in western Montana vary by sex and season (Murphy 1983). The smallest home ranges occur during winter with averages of 33 (17–73) and 26 (13–62) km^2 for males and females, respectively. During spring and autumn these expanded to 290 (176–484) and 132 (49–245) km^2. Similar values were observed for Idaho populations. Adult males and females only interact during the breeding season, and then only for a short period. Juveniles, however, will stay with their mother for 1.5–2 years learning how to hunt.

Partitioning of resources between mountain lions and sympatric populations of other predators such as bobcats and coyotes, occurs during the summer. Although bobcats and mountain lions share areas with denser cover, they tend to select different sized prey. Coyotes, on the other hand, forage in more open areas avoided by cats. However, during winter when heavy snows force many prey to lower elevations, direct competition may occur. Lions have killed coyotes and bobcats in Montana and Idaho (Boyd and O'Gara 1985), often when protecting a fresh kill, although sometimes for food. However wolves have treed and even killed mountain lions.

Populations of mountain lions in western Montana have been steadily rising over the past several years, with more frequent encounters between humans and lions. Lions are routinely sighted around Missoula and on many occasions have entered the city. Although mountain lions generally avoid human contact, several recent instances (1 fatal) have occurred in the state. Encroachment of human dwellings into prime mountain lion habitat and larger deer populations will only increase such encounters.

Reproduction: Breeding can occur anytime of year. Reported births occurred in all seasons except spring in western Montana (Murphy 1983), although studies in central Idaho indicated that most litters are born in spring or early summer. Males are polygynous. Gestation is from 82–96 days in duration. One to 6 [$\bar{x}$ = 2.4–3] young are born. At birth, eyes and ears are closed, and open at 1–2 weeks. Until the age of 3–4 months, young are densely spotted and have stripes on their upper forelegs. Weaning occurs between 1 and 2 months of age at which time the young weigh 3–4 kg. Before the 1st winter they weigh 13–14 kg. Yearlings reach 27–36 kg, and adult weight is attained between 2 and 4 years. Sexual maturity occurs between 2 and 3 years of age. Adult females breed every other year.

Status: Common. Mountain lion are regulated as a game species. Since 1989, the number of animals harvested has steadily increased, rising from just under 200 to over 530 in 1995.

Currier, M. J. P. 1983. *Felis concolor.* Mammalian Species 200:1–7.

Lynx
Lynx canadensis

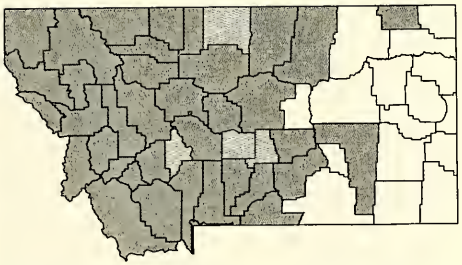
Lynx (*Lynx canadensis*). See plate 10.

Scientific Name: The lynx was first described by Carolus Linnaeus, in 1758, from specimens obtained near Upsala, Sweden. The 1st description of the lynx in North America was by R. Kerr, in 1792, from specimens collected in Quebec, Canada. Original names were *Felis lynx* and *Lynx canadensis* respectively, 2 names which have been periodically used for the past 200 years. Taxonomists still disagree about not only the relationship between North American and European populations, but also that between lynxes and other felids. Some suggest that both "*Felis*" and "*Lynx*" generic designation should be *Felis*, whereas others suggest that lynxes are sufficiently distinct to warrant their own genus, *Lynx*. When 2 species are recognized within the genus *Lynx* the European form is designated *Lynx lynx*, and the North American form is *Lynx canadensis*. The generic designation *Lynx* is the Greek word for "cat;" the specific epithet, *canadensis*, designates the type locality in North America.

Description: The lynx is the 2nd of 2 medium-sized felids in Montana, the other being the bobcat. Color is yellowish-gray to grayish-brown above with belly and throat white. Varying degrees of spotting occur in different populations. Backs of the ears are darker brown with a central silver-gray spot, and possess pronounced black ear tufts. A flared facial ruff decorates the chin. The short tail is tipped in black above and below. Long legs and a compact, short body give this species a unique body conformation. Fore- and hind feet are disproportionately large (10 × 10 cm), round, and heavily furred. The lynx may be confused with the other Montana spotted cat, the bobcat, particularly from a distance. In color, the lynx is grayer and has less marked spotting. For lynxes, the entire tail tip is black, while that of the bobcat is black only on the dorsal surface. Ear tufts in the lynx are twice as long as those of the bobcat. Differences in size of the feet and overall body proportions are so distinct that positive identification should be possible. Mountain lion cubs are spotted at birth and retain this mottling for many months, after which they reach and exceed the body size of lynx and bobcats. No difficulty should arise in distinguishing mountain lions from lynx and bobcats as the mountain lion has a long tail. Several distinguishing skull characteristics are also evident (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 925.0(2)/♀ 895.0(2); Ta ♂ 119.0(2)/♀ 95.5(2); HF = ♂ 255.5(2)/♀ 230.0(2); E = ♂ 85.0(1)/♀ 50.0(2); M [kg(*n*)] = ♂ 10.8(6)/♀ 8.4(6). Dental formula: i 3/3, c 1/1, p 2/2, m 1/1, total 28.

Distribution: The lynx is distributed across northern North America from west-



Map 84. Distribution of the lynx, *Lynx canadensis.*

ern Alaska to eastern Newfoundland, with historical extensions as far as Oregon, Idaho, Utah, Colorado, the Great Lakes, and New England. Southern populations use marginally suitable habitat. Since 1983, the status of many southern populations is questionable. Montana may have larger populations than any other western state.

Ecology and Behavior: The lynx is a denizen of the boreal forest. Eastward range extensions into Montana, Idaho, and Washington are associated with boreal forest at higher elevations. Until recently, only 5 studies had been conducted in western mountains, 2 in Washington and 3 in Montana, and these involved few individuals. However, a recent, long-term study was initiated in the Swan Mountains of western Montana by the United States Forest Service in conjunction with the University of Montana which should provide additional information. From these studies, a picture of the lynx existing at the fringes of its range can be developed.

The distribution and abundance of lynx are associated closely with those of their primary prey species, the snowshoe hare. In Montana, snowshoe hares are most abundant in young, dense stands of lodgepole pine. Radiotelemetry work in western Montana (Brainerd 1985; Koehler et al. 1979), illustrated that lynx use this habitat heavily. Activity is highest from evening to early morning. Animals move across their home range covering an average of 6 to 10 km. Foraging most often occurs by the animal periodically lying in "waiting beds" centered in areas of hare activity. When an unsuspecting hare happens by, the lynx is ready to pounce. Chases may ensue, but prey is usually captured within 20–50 m. Cooperative hunting may occur. During 1 such instance, 2 adults and a juvenile in Glacier National Park were observed to work a boulder field. One adult drew the attention of a Colombian ground squirrel, while the other snuck up and captured it (Barash 1971).

In the only study which directly addressed lynx food habits in the western United States, snowshoe hares occurred in 79% of scats, while red squirrels were found in 24% (Koehler 1990); 3% contained grouse and 3% ungulates, the latter likely consumed as carrion. Although mice were not identified in these scats, they probably are an important food source, particularly during summer and when snowshoe hare populations are in decline. In contrast to the early successional forests required for foraging, late successional stands are required for denning. Ground structure, in the form of large deadfall, is needed to provide both thermal and protective cover for kittens. Den sites in the western states are characterized by dense canopy closure and high density of downed trees which provide both horizontal and vertical structure. Denning sites are chosen in part due to their proximity to foraging stands. Either adjacency of both stand types makes the environment suitable for lynx occupancy or appropriate travel corridors (regions of closed canopy >2m in height) are interposed between foraging and denning habitats.

Snowshoe hares and lynx do not undergo the dramatic cycles in abundance at their southern limits, as they do in their northern ranges (Dolbeer and Clark 1975; Koehler 1990). Lynx populations in southern areas match the behavior of more northern populations during periods of low hare abundance. Snowshoe hare populations avoid the boom and bust "10 year cycles" because the number of predators is more stable. Whereas in northern regions, when hare populations are on the upswing and pred-

ator levels are depressed, allowing hares to disperse into suboptimal habitats and reproduce. In southern areas, hares which disperse into suboptimal habitats face other predators. The greater diversity of both predators and prey dampens the population cycles of hares and, as a result, lynx populations remain stable too.

Home range sizes are greatly influenced by seasonal food availability. In western Montana, summer average home range estimates (based on radiotelemetry) of 36 km^2 (n = 1; Koehler et al. 1979), 43.4 km^2 (n = 4; Brainerd 1985), and 125 km^2 (n = 6; L. F. Ruggiero pers. comm.) have been reported for males and 18.3 km^2 (n = 3; Brainerd 1985) and 42 km^2 (n = 2; L. F. Ruggiero pers. comm.) for females. Mean annual home ranges were 122.0 km^2 (n = 8; Brainerd 1985) and 220 km^2 (n = 4; L. F. Ruggiero pers. comm.) for males and 44.3 km^2 (n = 4; Brainerd 1985) and 90 km^2 (n = 2; L. F. Ruggiero pers. comm.) for females.

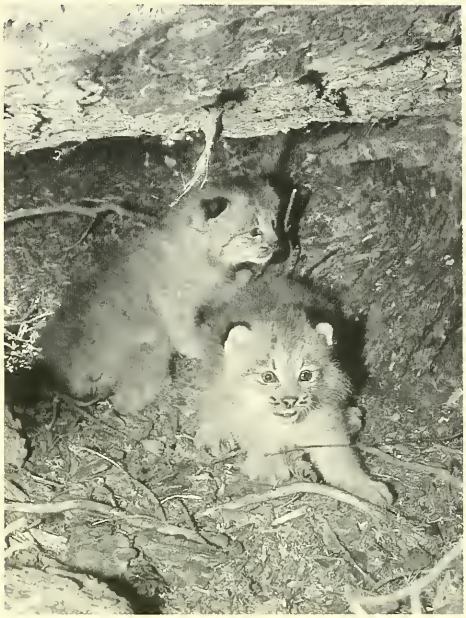


Fig. 64. Lynx kittens.

Reproduction: In Alberta, young begin to breed in March and April. Gestation is about 60–70 days with births likely in late May to early June. The size of juveniles in northcentral Washington in July suggests birth in late May, and conception between March and April (Koehler 1990). Litter sizes of lynx in Montana, based on placental scars, ranged from 1–5, with a mean of 2.75 (Brainerd 1985). Adult females have larger litter sizes compared to yearlings ($\bar{x}$ = 3.25 versus 1.75, respectively) and adult females also had significantly higher conception rates (100% versus 44%).

Neonates are born with closed eyes and ears and no teeth. Post-natal growth is rapid, however, with young walking by 24 days (Fig. 64). Meat may be eaten as early as 30 days although suckling may continue up to 6 months. Young remain with their mother for 10 months, when a new breeding season begins. Although females may attain sexual maturity at 10 months, most do not successfully breed until 22 months. Males do not reach sexual maturity until their 2nd year.

Status: The current status of lynx in Montana is not well understood. Technically, the lynx is a furbearer, with an annual quota of 2 individuals. Recent estimates place the statewide population at between 800 and 1,000. Historically, lynx were considered relatively common in western Montana, particularly in the Glacier National Park region (Bailey and Bailey 1918). Between 1959 and 1967, 990 lynx were legally trapped. Because of declining populations and concern throughout the northwest, stringent quotas were recently adopted. In 1995, a total of 5 animals were legally obtained, all in Flathead County.

Tumlison, R. 1987. *Felis lynx*. Mammalian Species 269: 1–8.

Bobcat
Lynx rufus

Bobcat (*Lynx rufus*). See plate 10.

Scientific Name: The bobcat was first described by Schreber, in 1777, from specimens obtained in New York. Rafinesque working in 1817 from notes and specimens collected by Meriwether Lewis during the famous Lewis and Clark expedition described this species in the northwest.

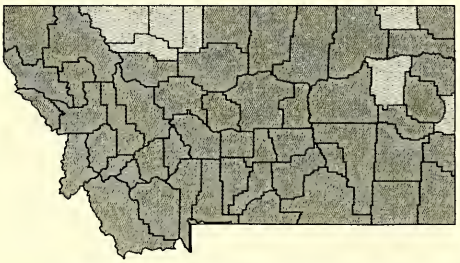
The generic designation *Lynx* is the from the Greek meaning "cat." The specific epithet *rufus* is Latin for "red."

Description: The bobcat is 1 of several North American "spotted cats," medium in size, with a distinctive color pattern which sets it apart from other Montana felids. One of the 1st descriptions of the species was provided by Meriwether Lewis on 21 February 1806 while he and his party resided at Fort Clatsop, on the Oregon coast. His observations are as clear and useful today as they were nearly 200 years ago:

"... this animal is about the size or reather larger than the wild cat of our country (the bobcat of the East coast) and is much the same in form, agility and ferosity. the colour of the back neck and sides is a redish brown irregularly variegated with small spots of dark brown the tail is about two inches long nearly white except the extremity which is black; it terminates abruptly as if it had been cut off. the belly is white with small black spots, beautifully variagated. the legs are of the same colour with the sides and back marked with transverse stripes of black the ears are black on the outer side covered with fine short hair except at the upper point which furnished with a pensil of fine, streight, black hair, ¾ of an inch in length. the fur of this anamal is long and fine, much more so than the wild cat of the United States but less so than that of Louservea (lynx) of the N. West." (parentheses are this authors; Moulton 1990: 333–334).

Lewis was describing a prime winter pelt at its fullest growth. In addition both fore- and hind feet are small, with the hind feet the smallest. From a distance, bobcats could be confused with the other medium-sized felid in Montana, the lynx (*Lynx canadensis*). Up close, however, they can be distinguished by color (the lynx is predominantly gray), degree of spotting (spots on the lynx are far less numerable and distinct), ear tufts (those of the lynx are long and showy), and size of feet (those of the lynx are disproportionately large). Several skull characteristics are diagnostic (Foresman 2001).

Measurements: [mm(*n*); ear measurements Hall 1981]: TL = ♂ 1041.8(10)/♀ 931.7(10); Ta = ♂ 166.5(10)/♀ 156.1(10); HF = ♂ 193.2(10)/♀ 179.9(10); E = ♂ 61–77/♀ 63–76; M [kg(*n*)] = ♂ 11.7(10)/♀ 8.5(10). Dental formula: i 3/3, c 1/1, p 2/2, m 1/1, total 28.



Map 85. Distribution of the bobcat, *Lynx rufus*.

Distribution: The bobcat is widely distributed across North America, extending from the southern regions of the Canadian provinces throughout the continental United States and Mexico.

Ecology and Behavior: The bobcat uses a wide variety of habitat types in Montana from semi-desert grasslands and shortgrass prairies, with sagebrush and juniper thickets, to riparian zones characterized by cottonwoods and willows. Dense coniferous forest stands of Douglas fir, ponderosa pine, lodgepole pine, and Englemann spruce are also used.

In all habitats, the bobcat needs cover and structural complexity not only for hunting but also for protection of nursery dens. In the forested mountains of the west, dense cover is abundant and nursery dens occur under large fallen trees, in the interstices of large boulders in talus slopes, or in rock fissures, caves, or abandoned mine shafts (Brainerd 1985). In the more open pine forests and sagebrush communities of central Montana, and the eastern shortgrass prairies, cover is provided by the broken terrain itself (Giddings et al. 1990). One den site was located in a steep road cut which had slid, forming a protective pocket heavily overgrown with fireweed (Knowles 1981). A 2nd was a small "cave-like hole" 4 m in depth, under a juniper bush. Dens in more structured habitat often have >1 opening and frequently 2 or more chambers. More permanent dens are only used to raise litters, at other times of the year bobcats move throughout their home range, often resting in transient dens in brushy thickets or under downed logs.

Most activity is nocturnal, although early morning and evening movements are common. Peak activity for 1 animal was between 0400–1000 hours and 1600–2000 hours (Brainerd 1985). Rabbits and hares make up a majority of the diet, although other small mammals such as voles and mice are eaten. Where prairie dogs are abundant in the north-central portion of the state, they are actively sought (Knowles 1981). Ground-nesting bird species, such as grouse and pheasant, are also taken frequently. The hunting strategy of this species is to wait patiently next to a game trail or a prairie dog colony for an animal to appear. A quick pounce is usually all that is required to dispatch the unsuspecting prey.

Home ranges in western regions of the state are some of the largest described for this species (Brainerd 1985). Males had a mean value of 111.4 km^2, while those for females averaged 61.5 km^2. As lactating females need to remain close to their litters, they have smaller summer home ranges than non-denning females (mean of 13.9 versus 22.2 km^2 respectively). In the central Montana breaks, a single male had a yearly home range of 83.3 km^2, while that of a female was 17.8 km^2 (Knowles 1981). Daily movements averaged 1–5 km. In eastern Montana, between Forsyth and Miles City, home range size was directly correlated with lagomorph abundance (Giddings et al. 1990; Risdahl 1988). During periods of high density, a single male had a home range of 4.3 km^2, while annual values for females ranged from 20.1–33.5 km^2. Following a 58-fold decline in lagomorph densities, males and females significantly increased their annual home ranges (♂ = 23.9–100.5 km^2; ♀ = 24.8–233.5 km^2) and the distances they moved daily (9–10.5 km).

Reproduction: Breeding begins in mid-February and continues until at least mid-April; females are seasonally polyestrous. Dens are established in early May and kittens are born between mid-May and ear-

ly June, after a gestation of 70 days. Average litter sizes for Montana populations, determined from carcass data (placental scars), varied from 2.69 (n = 413) to 2.1 (n = 57), the latter value occurred during a severe lagomorph decline. Average litter sizes for observed litters during moderate to high lagomorph populations were 2.7 (n = 10). Young are helpless at birth but grow quickly and may begin outside forays at 9–10 weeks of age. Weaning occurs at 2 months. Juveniles may stay with the mother until their 1st spring, and disperse as the breeding season begins.

Although females may reach sexual maturity during the 1st spring, most do not successfully produce litters until their 3rd summer. Males reach sexual maturity in their 2nd spring.

Status: Common; classified as a furbearer. Nearly 800 animals were harvested in 1995, a majority from northwest and northcentral regions.

Larivière, S., and L. R. Walton. 1997. *Lynx rufus*. Mammalian Species 563:1–8.

Family Mephitidae—Skunks*

Striped Skunk
Mephitis mephitis

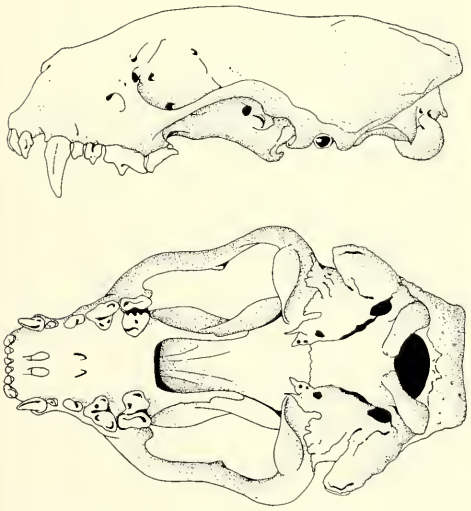


Fig. 65. Skull of a skunk (*Mephitis*).

Striped skunk (*Mephitis mephitis*). See plate 11.

Scientific Name: The striped skunk was first described by J. C. D. Schreber, in 1776, from a specimen obtained in eastern Canada (present day Quebec). The original designation, *Viverra mephitis,* was changed in 1795 to that used presently, although many taxonomic revisions occurred over the past 200 years. The generic and specific

* For representative skull characteristics of this taxonomic family refer to Fig. 65.

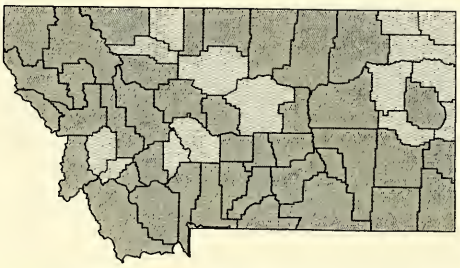
name, *mephitis,* is from the Latin mephit which means "bad odor," a reference to this species' well-known musky smell. The vernacular modifier denotes the obvious stripes along the dorsal surface; the term "skunk" may have originated from the Abenaki Indian (an Algonquin family) term "segankw" or "segongw."

Description: The striped skunk is 1 of the most easily recognized species in Montana. The distinctive black body color is bisected by 2 lateral white stripes which begin as a white patch on the back of the neck and extend to the rump. A white stripe is present on the nose and forehead, and white hairs may be scattered throughout the bushy tail. Considerable color variation exists, particularly in the degree of white patterning. One individual in the University of Montana museum is actually reddish-orange with white striping. A triangular-shaped head, rounded ears, shiny black eyes, and an overall body form which is stocky with short legs distinguishes it from members of the weasel family. Sexual dimorphism in body size occurs, with males 15% larger than females. Several skull characteristics are diagnostic (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 560.0(2)/♀ 712.0(4); Ta = ♂ 227.5(2)/♀ 261.3(4); HF = ♂ 69.0(2)/♀ 62.3(4); E = ♂ 21.5(2)/♀ 21.0(3); M [g(*n*)] = ♂ 3032.3(5)/♀ 2754.7(3). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: The striped skunk is found over nearly all of North America, from the southern boundary of the Northwest Territory of Canada, across all Canadian provinces and the continental United States into northern Mexico. The striped skunk is absent from Alaska and some desert regions of California, Nevada, and Utah.

Ecology and Behavior: The striped skunk occurs in a wide variety of habitats ranging from forest edges to brushy, more



Map 86. Distribution of the striped skunk, *Mephitis mephitis.*

open grasslands, particularly where rock outcrops exist. In Montana, it frequents cultivated lands where it uses fencerows as travel corridors. Dens may be either dug or taken over from those of marmots, badgers, or coyotes. Outbuildings around farms and ranches provide ideal cover, and many animals construct dens under such foundations. One to 2 entrances are common.

Animals are primarily nocturnal during the warmer months, foraging most often 1–2 hours after sunset, with activity tapering off over the night. Individuals travel extensively each night, upwards of 3 km. Activity is greatly reduced during extreme cold temperatures. To offset the cold, females will den communally, and a male may also be included, although males do join other males. Body fat is stored, and striped skunks can enter a shallow, lethargic state to reduce metabolic costs. The mean active winter body temperature of 37.7°C may be lowered to 28.4°C as the animal enters torpor.

Home range size varies with habitat availability and is 87–543 ha for females and 98–688 ha for males in an area of North Dakota which was 80% cultivated. Values for Illinois farmland are similar. Larger home ranges occur during spring when reproduction begins. In western Montana, on Nine Pipes National Wildlife Refuge, population density was 7.1/km^2 (Pengeroth 1991). Striped skunk populations are routinely skewed toward younger individuals. Few individuals are >4 years of age and 64% of animals captured during 1 year were <2 years old (Pengeroth 1991).

The striped skunk is primarily insectivorous, although it is quite opportunistic, and omnivory is common. The long list of items includes grasshoppers, beetles, lepidopteran larve, voles, and mice. Plant material is also eaten when available, particularly fruits such as blueberries, black cherries, and apples. Significant predation on nesting waterfowl, in particular mallards, has occurred on Ninepipe National Wildlife Refuge (Hall 1994). Ninety-seven percent of nest failures during 1986–1987 were due to predation, primarily by striped skunks. The removal of striped skunks contributed to a tripling of mallard nest densities by 1990.

The strong odor of the striped skunk is well known, if not personally experienced, by nearly everyone. Two small glands 1.25 cm in diameter and heavily invested in muscle, lie in the anal region, with nipples exiting at the anal opening. The nipples are exposed when the tail is raised. About 15 ml of a greenish-yellow, oily secretion, is produced by and stored in these glands, and can be released under voluntary control either as an atomized spray or in a more concentrated stream. In the 1st detailed description of this secretion Blackman (1911: 491) stated: ". . . not only does the secretion reach the perfection of nauseating fetidity but the mechanism of effectively directing its discharge has reached the highest degree of development. The animal is able not only to retain or discharge the secretion at will but also to eject it, for as great a distance as eight or ten feet and in any desired direction. . . ." The odiferous components of this secretion are mercaptans, containing trans-2-butenyl methyl disulfide and trans-2-butene-1-thiol, 3-methyl-1-butanethiol compounds (Anderson and Berstein 1975). Striped skunks spray as a last resort. First they stamp their forefeet loudly and flair out their tail producing an amazing display. They may even stand on their front feet and walk with their tail held high for a short distance. If such behaviors fail to discourage harassment, they will ultimately spray by turning their body so that their glands and head are facing the object of concern. To remove this scent from clothes, or the family pet, use a dilute solution of sodium hypochlorite (the active ingredient in household bleach), or equal parts of oil of citronella and oil of bergamot, on animals and humans (Schwartz and Schwartz 1959). Clothes can be soaked in ammonia, gasoline, or left outside in the sunlight. However, no remedy is particularly effective.

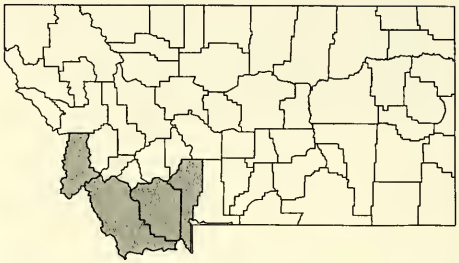
Reproduction: Breeding in Montana spans from early March through early June (Pengeroth 1991). Most conceptions occur in late March; and later conceptions are usually in response to loss of the 1st litter. Ovulation is induced by copulation as in all mustelids. As implantation may be delayed, gestation varies from 59–77 days. Conception earlier in the breeding season results in a longer total gestation. Parturition occurs in May or early June. A single litter is produced each year; mean litter sizes reported for wild populations range from 5.8 to 7.8. Reproductive output in western Montana populations, calculated as the number of embryos/female, was 6.71 ($\pm$0.34 *SD*) (range = 1–14—Pengeroth 1991). Young at birth weigh 32–35 g and can produce musk, although this material is not actively expressed until the eyes open at 3 weeks of age. Weaning occurs by 8 weeks but adult body size and reproductive maturity does not occur until 10 months.

Status: Common and locally abundant; classified as a furbearer. Although pelt prices have remained low recently, nearly 1,800 individuals have been trapped yearly since 1989. In 1986, nearly 9,000 animals were taken.

Wade-Smith, J., and B. J. Verts. 1982. *Mephitis mephitis.* Mammalian Species 173:1–7.

Western Spotted Skunk
Spilogale gracilis

Scientific Name: The western spotted skunk was first described by Carolus Linnaeus (1758) who placed it in the genus *Putorius*, based on a specimen collected in South Carolina. In 1890, C. Hart Merriam (1890) suggested the generic name of *Spilogale*, which is in current usage today. Two distinct species are distinguished in the United States (Mead 1968). *Spilogale putorius*, the "eastern" spotted skunk, occurs in eastern and central regions of the country, while *Spilogale gracilis*, the "western" spotted skunk, occurs from Wyoming to central Texas westward. The generic designation *Spilogale* is from the Greek composite spilos which means "spot" and galee which means a "weasel-like" animal. The specific epithet *gracilis* is Latin for "slender." The vernacular name is derived from the prominent spotted color pattern. The western spotted skunk is also referred to as the "civet cat."



Map 87. Distribution of the western spotted skunk, *Spilogale gracilis*.

Description: Both species of spotted skunk may occur in Montana, and they are hard to tell apart although the eastern spotted skunk may be slightly smaller and may lack white hairs on the tip of its black tail. The western spotted skunk is slender in body form, with short legs, a narrow triangular-shaped head and a bushy tail which is about equal to its body length. Its body color is dark black, broken by distinctive white bars along the back and sides as though stripes had been interrupted. Its forehead has a small white patch. The western spotted skunk would be difficult to distinguish from the eastern spotted skunk if indeed the eastern spotted skunk is in Montana. Here only the difference in terminal white hairs on the tail (present in the western spotted skunk and lacking in the eastern spotted skunk) might be helpful. However, if both species do exist, they would not be sympatric, thus location may help in identification. The western spotted skunk should not otherwise be easily confused with any other Montana mammal. It is clearly distinguished by its color pattern and body size (0.5 times that of the striped skunk).

Measurements: [mm(n), from Washington animals]: TL = ♂ 411.6(10)/♀ 387.5(6); Ta = ♂ 122.1(10)/♀ 115.7(6); HF = ♂ 50.1(10)/♀ 47.3(6); E = ♂ 27(1)/♀ 28(1); M [g(n)] = ♂ 632.8(10)/♀ 451.3(6). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: The western spotted skunk ranges from the southwestern edge of British Columbia, through the northern half of Central America, eastward as far as a line extending from eastern Wyoming through central Texas. In Montana, only 5 records exist. The 1st specimen was obtained in Tin Cup Canyon, Ravalli County in 1929 (Jellison 1931). Additional specimens have now been recorded from Medicine Springs, Ravalli County in 1945 (Jellison 1945), in the Ruby Range of Madison County, south of Dillon in Beaverhead County, and south of Bozeman in Gallatin County, thus it is probable that the western spotted skunk is only distributed along the southwestern region of Montana (Hoffmann et al. 1969).

Ecology and Behavior: Little information has been reported on the ecology of

the western spotted skunk. Most available information comes from studies conducted on eastern populations prior to 1968, when only 1 species was recognized (Crabb 1948). With few exceptions, this information is probably just as valid for the western species and, since both species may occur in Montana, these earlier studies are excerpted here.

The western spotted skunk prefers wooded, brushy habitat where good ground cover exists. The few specimens collected in the state have all come from such areas. Although the eastern spotted skunk is described as avoiding wetlands, in southeastern Washington (Dalquest 1948) and Idaho (Davis 1939) western spotted skunks are commonly found in riparian areas. They are insectivorous although a wide variety of small mammals, birds, and plant material are consumed, especially during winter. Thus the western spotted skunk, like the striped skunk, is much more omnivorous than other Montana carnivores. They have long claws and use these to readily climb into trees where they may forage.

Western spotted skunks are most active at night, year-round, and are thus rarely observed. Den sites, under logs, rock piles, or outbuildings may be used by >1 individual, and >1 den may be visited. Burrows previously dug by other species, such as ground squirrels or striped skunks, may also be used.

The western spotted skunk is much smaller, quicker, and more agile than the striped skunk; Seton (1929:398) referred to them as "animated checkerboards." Although western spotted skunks may try to bite when 1st restrained, their general demeanor is docile. The author has maintained a large number of individuals in captivity for research and found them to be easily handled. Many animals raised in captivity were not descented and made no attempt to spray when handled gently.

One of the most interesting and unusual behaviors for which western spotted skunks are well-known is "handstand" display when confronted. While balancing on its fore-feet the animal arches its back and turns its hindquarters so that it can both see its opponent and point its anal glands in that direction. The western spotted skunk can readily spray its scent in this position and then resume running.

Although the western spotted skunk has been trapped for its pelt, in Montana it is so uncommon that it probably is not reported by trappers.

Reproduction: Spermatogenesis begins early in spring, although it does not peak until late September. Females come into estrus in late September and the breeding season extends until early October when testicular regression begins. Implantation is delayed after conception. Embryos reach the blastocyst stage (about 400 cells) by early October and lie dormant in the uterus until mid-to-late April. Embryos implant at this time and about 30 days later birth occurs. Thus parturition is in mid-to-late May (Mead 1968, 1995).

Eastern spotted skunks do not delay implantation. They mate between March and April, and litters are born in late May to early June, after a 45–55 day gestation. Since the eastern spotted skunk mates in spring, and the western spotted skunk mates in the autumn, the 2 are reproductively isolated.

Litter sizes in the western spotted skunk range from 2–5 ($\bar{x}$ = 3.8). Young mature rapidly and are weaned at 7 weeks of age. Juvenile males may actually reach sexual maturity at 3–4 months of age.

Status: Unknown. Only 5 specimens have been recorded in the literature, the most recent of which occurred over 30 years ago. If this species still occurs, it should be considered rare.

Family Mustelidae—Mustelids*

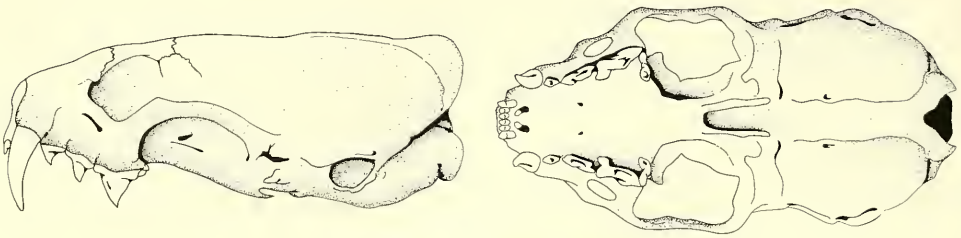


Fig. 66. Skull of a weasel (*Mustela*).

Wolverine
Gulo gulo

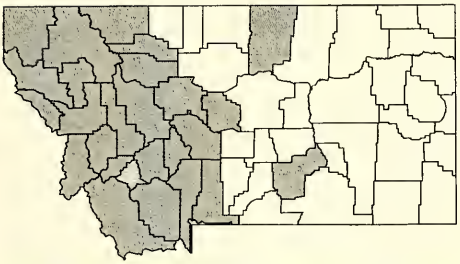
Scientific Name: The wolverine was first described by Carolus Linnaeus, in 1758, from specimens obtained near Hudson Bay, Ontario. Initially identified as *Ursus luscus,* the generic designation was changed to the current name, *Gulo,* in 1823 (thus *G. luscus*). The Old World (Eurasian) form was originally considered a distinct species and was accordingly identified as *Gulo gulo.* A detailed comparison of European and Alaskan specimens concluded that only 1 species was justified and the name *Gulo gulo* had precedence. The word gulo is derived from the Latin meaning "a glutton."

Description: The wolverine is the largest terrestrial mustelid in Montana. In body conformation it resembles a small bear, thus Linneaus' original generic designation of *Ursus.* It has a solidly compact body, broad head supported by a short neck, short legs, and a bushy tail. Its feet are proportionately large and contain sharply curved, robust claws. The pelage consists of a dense underfur, woolly in consistency, and coarse guardhairs. Body color varies from dark brown to black, with distinctive blond to reddish bands of fur extending from the lateral portion of its shoulders posteriorly and converging across its rump. Although highly variable, white to yellowish throat markings are often present. The only mustelid that resembles the wolverine is the fisher, which is about half the size and does not have a light colored lateral stripe.

Measurements: [mm(*n*); Copeland and Harris 1984; Smith 1993]: TL = ♂ 995.0(4)/♀ 875.0(4); Ta = ♂ 186.3(4)/♀ 186.7(3); HF = ♂ 170.8(4)/♀ 160.0(3); E = ♂ 56.3(3)/♀ 43.0(1); M [kg(*n*)] = ♂ 12.3(8)/♀ 7.7(18). Dental formula: i 3/3, c 1/1, p 4/4, m 1/2, total 38.

Distribution: Although historically distributed throughout Alaska, Canada, and the northern continental United States, with extensions along the Rocky Mountains into Arizona and New Mexico, the range of the wolverine has declined dramatically in recent years. Currently wolverines live from Alaska, across the Northwest Territories, and as far north as the Arctic archipelago, British Columbia. They also extend across northern portions of the remaining Canadian provinces, with extensions into Washington, Idaho, Montana, Oregon, Utah, Wyoming, and Colorado. Montana and Idaho are the only states outside of Alaska that are thought to have significant numbers.

* For representative skull characteristics of this taxonomic family refer to Fig. 66.



Map 88. Distribution of the wolverine, *Gulo gulo*.

Ecology and Behavior: In Montana, the wolverine lives in several coniferous montane forest types. In most of the western one-third of Montana grand fir, alpine fir, Douglas fir, lodgepole pine, ponderosa pine, and western larch dominate the landscape. Seventy percent of the radiotelemetry locations from a population in western Montana were in alpine fir forests with scattered mature timber. In Idaho subalpine cirque habitats were of primary importance (Copeland and Harris 1994). Talus fields in such cirques were used for thermal cover, as a source of small prey species, and for den sites. Habitats with rugged, roadless, isolated, "wilderness" conditions are most preferred. In Montana, Idaho, and British Columbia higher elevations are chosen during summer.

Wolverines are often described as "nomadic" in behavior; traveling widely across the landscape in search of food or, during the breeding season, potential mates. Activity may be primarily nocturnal or more irregular with animals alternating between rest and activity throughout the day. Use of remote sensing cameras by the author documented wolverines in the Bitterroot Mountains (Bitterroot National Forest) on 2 occasions, and at the base of the Rattlesnake Mountains (Lolo National Forest) once, all 3 incidents occurring during daylight hours (Fig. 67). Average daily movements in central Idaho ranged from 3.4 (♀) to 7.9 (♂) km (Copeland and Harris 1994). Maximum movements over a 3-day period in western Montana were 64 km for males and 38 km for females. Mean home range size for males was 422 km^2 in Montana, and

Fig. 67. Wolverine captured by remote-sensing camera in the Bitterroot Mountains of western Montana.

2,079 km^2 in Idaho; for females these values were 422 km^2 and 423 km^2 respectively.

Elevational shifts in activity are likely a response to food availability. Wolverines hunt or scavenge a wide variety of animal species. In summer, high elevation rock slopes provide a bounty of small mammals such as Columbian ground squirrels and marmots, while adjacent forested areas provide snowshoe hares, mice, voles, and porcupines. Insects and numerous plant materials also have been found in scat samples. As deepening snows reduce food abundance at higher elevations, wolverines move down in search of carrion. Scat analyses from populations in Montana and Idaho showed that 80% and 74%, respectively, contained ungulate material (primarily elk, deer, and caribou).

As with most mustelids, the wolverine is solitary. Males and females only associate during the breeding season; females will remain with their kits during the 1st summer following their birth. No well-defined pattern of territoriality occurs. On the contrary, the wolverine's foraging strategy (scavenging), and requisite large home range, precludes its ability to maintain a strict territory.

By 1920, the wolverine was near extinction in Montana (Newby and Wright 1955). Beginning in the late 1930s, increased sightings were reported in the Glacier National Park region, and by the late 1950s their range had extended into the southwest (Newby and McDougal 1964). This increase is thought to have continued through the 1980s.

Reproduction: Testicular recrudescence begins in January with maximal size reached by late March or early April. Peak spermatogenesis occurs in late May to early June. Initial ovarian activity in females occurs in late May, although estrus begins in mid-June and extends into July. Testicular regression begins in late July or early August, thus the breeding season extends from June to August. Males locate estrous females and remain with them for 2–3 days.

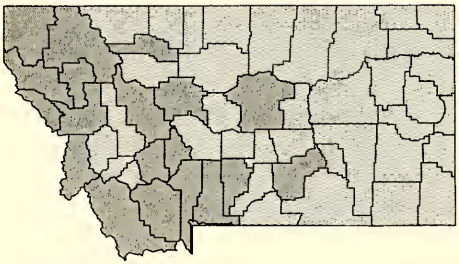
Natal dens are found within large boulder fields, under log jams, or under snow-covered tree roots, often in high elevation cirques. Litter sizes range from 1–5 based on unimplanted blastocysts, embryo, or fetal counts. Young are born with closed eyes and ears. They are raised in the natal den for the first 3 weeks when they are moved to a rearing den. New rearing dens are used about every 2 weeks. Growth is rapid with weaning at 7–8 weeks. Active movement away from the den begins at 12–14 weeks. Females reach sexual maturity at 12–14 months of age. Males attain sexual maturity at 2+ years of age.

Status: Uncommon; classified as a furbearer with limited annual harvesting. In 1995, 12 animals were harvested.

Pasitschniak-Arts, M., and S. Larivière. 1995. *Gulo gulo*. Mammalian Species 499:1–10.

Northern River Otter
Lontra canadensis

Northern river otter (*Lontra canadensis*). See plate 11.



Map 89. Distribution of the northern river otter, *Lontra canadensis*.

Scientific Name: The northern river otter was first described by Schreber, in 1776, from specimens obtained in Quebec, Canada. Originally identified as *Mustela lutra canadensis,* the nomenclature *Lutra canadensis* was applied by Sabine, in 1823, and has been commonly used until recently. The generic designation *Lontra* has now been applied and is used here. *Lontra* is derived from "Lontre," the Italian name for the otter. The specific epithet *canadensis* refers to the origin of the first described specimens.

Description: The northern river otter has the streamline shape of aquatic or semi-aquatic animals. The body is long and cylindrical with a robust, long, and rounded tail. Eyes and ears are small, the latter rounded. The broad head tapers through the neck to the shoulders without a noticeable constriction. Fore- and hindlimbs are quite short and muscular, and digits are broadly webbed. An extremely dense underfur is mixed with coarse guard hairs. Color is consistently a dark, rich brown, although the throat, chest, and venter are light brown to grayish. Dental formula is unique with 36 teeth. The northern river otter is easily identified and clearly distinguished from all mammals in Montana. The only other semi-aquatic mammals are the beaver and the muskrat. Both of these animals are rodents and thus have different skulls and dentition (Foresman 2001). Additionally, the river otter can be distinguished by its long, round, and quite robust tail which tapers posteriorly.

Measurements: [mm(*n*)]: TL = ♂ 1198.8(4)/♀ 1180.0(2); Ta = ♂ 485.0(4)/♀ 480.0(2); HF = ♂ 127.3(4)/♀ 127.5(2); E = ♂ 17.5(2)/♀ 19.5(2); M [kg(*n*)] = ♂ 9.5(4)/♀ 8.1(2). Dental formula: i 3/3, c 1/1, p 4/3, m 1/2, total 36.

Distribution: The northern river otter was historically distributed from Alaska and all Canadian provinces southward across the continental United States. More recently, heavy trapping pressure, riparian habitat destruction, and pollution have led to significant declines in the continental United States. The northern river otter is now extinct in 7 states. River otters are being reintroduced into many regions across the country.

Ecology and Behavior: The northern river otter is 1 of the most aquatic of mustelids, spending its life along riparian zones throughout North America. Although a va-

riety of aquatic habitats are used, from streams of the Alaskan tundra, to salt water estuaries of the coasts, northern river otters appear to select particular waterways in the intermountain west. In Montana and Idaho, northern river otters prefer waterways which are narrow and provide extensive edges in relation to open water. Prevalence of waterway obstructions (logjams, beaver ponds, marsh vegetation) and bank cover (>25%) enhance suitability, as does water quality and freedom from disturbance (Dronkert-Egnew 1991; Melquist and Hornocker 1983; Zacheim 1982). Such characteristics provide ample rest sites and may be suitable for den construction. Streams with damaged shorelines (usually due to overgrazing of adjacent land) are avoided (Zacheim 1982). Highly branched watercourses which meander through riparian areas and are surrounded by profuse bank cover are ideal for summer usage (Dronkert-Egnew 1991). During winter, larger river systems, with straighter courses which retain open water, are used when the smaller, slow moving streams freeze over.

Northern river otters most frequently use abandoned bank or lodge dens of beaver or muskrat. Alternatively they will rest away from the stream (50 m or more) in natural cavities such as depressions left when trees are uprooted, or in other burrows, such as those of foxes or coyotes.

The streamlined body and tail, and short, powerful legs allow northern river otters to glide through water much like a seal. Movement is by body and tail undulations with occasional kicks from the webbed hind feet. Cuticular scales on the dense fur allow individual hairs to interlock and entrap air and provide an extra layer of insulation when the animal submerges. These aquatic specializations allow northern river otters to feed almost exclusively on fish. Scat analyses have shown that 3 species of fish (kokanee salmon, mountain whitefish, and large-scale suckers) are preferred, and that most fish were adults >30 cm in length. Aquatic invertebrates are also eaten, as are birds (ducks), and mammals (muskrats) to a much lesser degree.

Daily activity varies seasonally. During spring and summer, activity is rhythmic with peaks occurring just before or after midnight, and near dawn. A similar pattern occurs in autumn, although active periods are longer. In winter, animals are more active during daylight hours, but considerable nocturnal movements still occur. Home ranges of males and females overlap extensively and are shaped by the nature of a specific drainage. An individual's home range may span a considerable length of river. Lengths of 8–78 km were measured for animals in central Idaho (n = 19; Melquist and Hornocker 1983), 15–58 km for those in northwestern Montana (n = 5; Dronkert-Egnew 1991). Within the home range northern river otters spend the most time often associated where fish spawning beds occur.

Northern river otters are more social than most mustelids. Family units encompass an adult female and her offspring. Young adult males may associate with adult females during the non-breeding season, but during the breeding season male–female associations are limited to breeding activity. Family groups remain together for 7.5–11.5 months when juveniles begin to disperse. After leaving their mother littermates often remain associated with one another for some time.

Reproduction: In Idaho and Montana breeding begins in April (Dronkert-Egnew 1991; Melquist and Hornocker 1983), and may extend into May, or even early June. After conception embryonic development is arrested at the blastocyst stage for 8–9 months. The small balls of cells than implant into the walls of the uterus and development continues about 62 days, with young born between March and May. Thus the total pregnancy lasts for 11 months. Females come into estrus shortly after parturition and may remain in heat for 7 weeks.

Mean litter sizes calculated from fetal counts varied from 2.29–2.75. In Idaho 2.4

pups/breeding female are produced (Melquist and Hornocker 1983). Young are weaned toward the end of summer at 5 months of age and may disperse at this time or remain with the female through the winter. In either case, dispersal is completed before the following breeding season. Both sexes reach reproductive maturity at 2 years of age.

Status: Significant populations in the western region; classified as furbearers and regulated by a yearly trapping season. One otter/trapper is allowed in each fur trapping district. In 1995, 102 individuals were harvested.

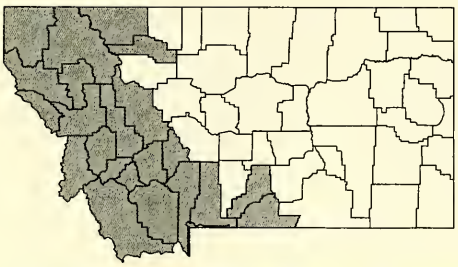
Larivière, S., and L. R. Walton. 1998. *Lontra canadensis.* Mammalian Species 587:1–8.

American Marten
Martes americana

American marten (*Martes americana*). See plate 11.

Scientific Name: The American marten was first described by W. Turton, in 1806, from specimens obtained in eastern North America. Originally designated as a member of the genus *Mustela,* the current name, *Martes americana,* was first applied, in 1912, by G. S. Miller. The generic designation *Martes* is Latin for "marten." The specific epithet *americana* designates the country from which this species was described and is used to separate it from the Eurasian marten, *M. martes.*

Description: The American marten has the typical "weasel" shape, a long, slender body with short legs and a long, bushy tail. The head is distinctly triangular in shape, and the ears are distinctive and rounded. Pelage is lustrous, ranging in color from light brown with a yellowish cast to nearly black. The American marten is distinctly marked with a throat and chest patch of light yellow to bright reddish orange fur. The pattern and color of these markings are highly individualistic. Males are typically two-thirds times heavier and somewhat larger in body length than females. The American marten is also referred to as the pine marten or American sable. Both names cause confusion as "pine marten" is most commonly applied to the Eurasian marten, and "sable" is more often used for *Martes zibellina,* an inhabitant of Scandinavia through eastern Siberia. The distinct shape of the head and the color of the throat distinguish this species from all others in the state, although several mustelids are similar. The mink is similar in size, but is most often a darker brown to black and has a small, irregular white throat patch rather than a yellow/orangish one. The mink's tail is also less bushy and its fur is shorter. The long-



Map 90. Distribution of the American marten, *Martes americana.*

tailed weasel is similar in color, but considerably smaller in size and lacks the long coat and bushy tail. Lastly the fisher is black in color with a white throat patch and is 3–5 times bigger than the American marten. Skull characteristics can also be used to separate these species (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 557.6(5)/♀ 549.1(8); Ta = ♂ 186.8(5)/♀ 170.4(8); HF = ♂ 83.8(4)/♀ 76.6(8); E = ♂ 41.7(3)/♀ 33.5(4); M [kg(*n*)] = ♂ 879.5(10)/♀ 568.2(10). Dental formula: i 3/3, c 1/1, p 4/4, m 1/2, total 38.

Distribution: The American marten is tightly associated with boreal forests and as such occurs across the northern region of North America. Its range extends from Alaska through the Canadian provinces with extensions through Washington, Oregon, California, and along the Rocky Mountains to Colorado and New Mexico. Populations also occur in northern regions of Maine, Vermont, New York, and Minnesota, and reintroduction efforts are being made in Wisconsin and Michigan.

Ecology and Behavior: The American marten is 1 of the most common, mid-sized forest carnivores in northern North America. Although populations have been reduced by loss of habitat and heavy trapping, the American marten is still common, particularly in western Montana. Mesic coniferous forests dominated by subalpine fir, Douglas fir, and lodgepole pine support the American marten in Montana, particularly stands at late successional stages. Structural complexity at ground level is important for protection, thermal cover, and providing habitat for prey species. Such cover (shrubs and coarse woody debris which develops from forest decay) is more abundant in older age stands. Marten live in talus fields above treeline, but these individuals probably need access to the forested interface.

The physical structure of older-aged forested stands provides natal and maternal den sites as well as resting sites. Trees, logs, snags, and rock outcroppings are most commonly used. Natal sites, those in which birth occurs, are often in tree cavities in locations with more cover than those chosen for maternal sites. Maternal dens, where kits are raised, are generally on the ground. Red squirrel middens or tree boles are used as daily resting sites during warmer periods. As temperatures decrease, martens take refuge in subnivean spaces provided by coarse woody debris under the snow. Marten must adapt behaviorally to colder temperatures because their long, thin shape, concomitant increased heat loss, and inability to deposit significant fat stores are particularly constraining physiologically during such periods.

American martens are active throughout the year with diurnal activity during summer months and more nocturnal activity during winter. While foraging, animals investigate any structure which may hide prey. They move rapidly across their home range using downed logs as runways, and periodically stop to poke into crevices and brush piles. Marten are dietary generalists, eating a wide variety of vertebrates and plant materials and having distinct seasonal preferences. In spring and summer small mammals, birds (as well as nestlings and eggs), and insects make up most of the diet. American martens will eat berries and fruits as they develop in autumn (huckleberry and raspberry are especially preferred). In winter, American martens are particularly adept at foraging under the snow in the subnivean space provided by

complex ground cover. Here they feed predominantly on voles and mice (in particular the red-backed vole, montane and meadow voles, and the deer mouse). Snowshoe hares and red squirrels are also important winter prey. In Montana nearly 74% of scats contained mice and voles, while 12% contained squirrels (Weckwerth and Hawley 1962).

Home range sizes vary with available habitat and prey abundance. In Montana home range sizes for males are 1.5–68 km^2 and for females are 0.4–7.2 km^2 (Burnett 1981; Coffin 1994; Fager 1991; Hawley and Newby 1957). Smaller values are from populations in denser forested stands, while larger values are from more open forest–grassland mosaic habitats.

Reproduction: The breeding season extends from late June to early August with a peak in July. Estrus lasts 1–4 days and may occur at intervals until the female conceives. When embryos reach the blastocyst stage their growth is suspended for 7–8 months. Implantation and renewed embryonic development occurs in February to March with a postimplantation period of 27 days. In Montana births occur in March or April. Litter sizes range from 1–5, with a mean of 2.7–3.0. Their eyes open by days 34–38, and weaning occurs by day 42. Juveniles probably do not disperse until August.

Sexual maturity is reached by 24–27 months in females. Males may attain sexual maturity earlier (at 15 months), although most successful breeding does not occur until 24–39 months.

Status: Common; classified as a furbearer with a trapping season in December. In 1995, >1,100 individuals were harvested.

Clark, T. W., E. Anderson, C. Douglas, and M. Strickland. 1987. *Martes americana.* Mammalian Species 289:1–8.

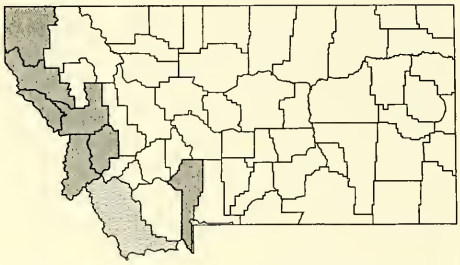
Fisher
Martes pennanti

Fisher (*Martes pennanti*).

Scientific Name: The fisher was first described by J. C. P. Erxleben, in 1777, from specimens collected in Quebec, Canada. Originally identified as *Mustela pennanti,* C. H. Smith was the 1st to use the current name in 1843. The generic designation *Martes* is Latin for "marten." The specific epithet *pennanti* honors the British naturalist Thomas Pennant who authored a text entitled *Arctic Zoology,* in 1771, in which North American mammals were described.

Description: The fisher is a mid-sized mustelid somewhat stockier in build than the American marten, although still having the long body form and short legs of the family. The long, bushy tail is more cylindrical than that of other Montana mustelids. Color is uniformly dark blackish-brown to black across most of the body surface.

Occasionally, some white spotting occurs on the venter, particularly on the chest. Lighter tipped guard hairs are numerous on the head and neck, providing a grizzled appearance. Males are 15% larger than females in length and may be twice as heavy. The fisher should not be confused with any other species in Montana. Body size and color distinguish it from other mustelids such as the mink, American marten, and wolverine.



Map 91. Distribution of the fisher, *Martes pennanti.*

Measurements: [mm(*n*); range of measurements Hall 1981]: TL = ♂ 980–1033/♀ 830–900, MT 877.5(4); Ta = ♂ 381–422/♀ 340–380, MT 328.7(3); HF = ♂ 113–128/♀ 89–115, MT 109.3(4); E = ♂ none/♀ 40.3(4; MT); M [kg(*n*)] = ♂ 4.4(10)/♀ 2.0(10). Dental formula: i 3/3, c 1/1, p 4/4, m 1/2, total 38.

Distribution: The fisher was historically distributed across a band of North America primarily centered through the Canadian provinces, south of the Northwest Territories. Three extensions into the continental United States occurred, 1 along the west coast into southern California, a 2nd through the intermountain region along the Rocky Mountain chain, and a 3rd covering a large portion of the northeastern half of the country. Heavy trapping and habitat destruction since the early 1800s reduced the range significantly, particularly in the east. By the 1930s, fisher were extinct in Montana. Between 1959 and 1960 reintroduction efforts were made in the western portion of the state (specifically in Lincoln, Missoula, and Granite counties). Additional reintroductions were made into the Cabinet Mountains, along the Idaho border, between 1988 and 1991. Recently, individuals have been observed in the Bitterroot Mountains south of Missoula. The current status of these populations is unclear.

Ecology and Behavior: The fisher inhabits a variety of forest types and is associated with conifer stands, mixed-conifer forests, and northern hardwood forests. In the west, late successional coniferous forests, usually dominated by Engelmann spruce and Douglas fir, are preferred. Riparian zones and habitats with high canopy closure are also chosen. The structural complexity of the forest is primary importance. Coarse woody debris, snags, and fallen trees set in a patchwork of late successional stands, with a range of tree sizes, provide the requisite environment for protective cover, and will support adequate numbers of prey.

Natal and maternal den sites are chosen for the protection they afford. Most sites occur in cavities within large living or dead trees. The single natal den found in Montana was in a large hollow log measuring 11 m. Several den sites may be used by a female as her litter develops. The initial movement from natal to maternal dens occurs 8 to 10 weeks after parturition.

Fishers eat a wide variety of small mammals, birds, carrion, and berries. Snowshoe hares are an important food for Montana fishers, as is deer carrion. Porcupines are also frequently eaten. The fisher is highly adept at killing porcupines and is 1 of only 2 predators that routinely do so (the other being the mountain lion). Mice and voles, in particular the deer mouse, red-backed vole, and meadow vole, are the most common small mammals eaten; red squirrels and northern flying squirrels are also taken in Montana. Foraging may occur anytime during the day or night, although peaks may occur at dawn or dusk. During colder periods, fisher are less active at night. Fishers move 5–6 km daily. Dispersing individ-

uals, or those recently introduced into an area may, over several days, travel up to 163 km (individuals transplanted to Montana). Fishers rest in tree cavities, snags, and squirrel nests among other sites in late successional forests. During winter, thermal cover is necessary for resting sites.

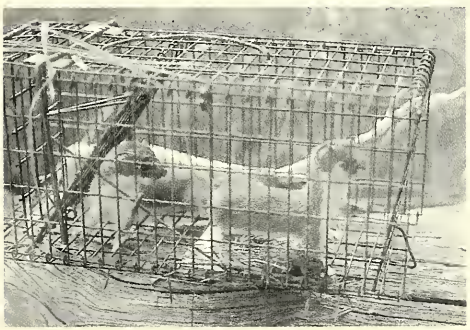
Home range sizes are influenced by available habitat and food abundance. In Montana, reintroduced individuals, and in Idaho, native animals have similar home range values (Heinemeyer 1993; Jones 1991). Average home range size for males ranged from 79 to 85 km^2 ($n = 8$). Female home ranges were more variable: from an average of 17 km^2 ($n = 7$) in Montana to 32 km^2 ($n = 4$) in Idaho. Home ranges may overlap considerably between sexes, but not between individuals of the same sex.

Reproduction: Breeding probably occurs from mid-March through April. Testicular recrudescence occurs in males in February, 1 month before females enter estrus. Delayed implantation occurs following conception with embryos remaining dormant for 9.5 months. Implantation and renewed development occurs in mid-to-late February with parturition between mid-March and early April. A post-partum estrus occurs within 3–9 days after parturition, thus wild females are continually pregnant. One to 4 altricial young are born ($\bar{x} = 2–3$). Development is slower than that of other mammals of similar size. Eyes open at 48–55 days, near the time of weaning. Young leave the den and begin exploring their external surroundings at 7–8 weeks of age, dispersing between 12 and 15 weeks. Young become reproductively mature at 12 months.

Status: Uncommon; classified as a furbearer with a harvest limit of 10 animals in each of 2 districts. Six animals were trapped in 1995. Efforts have recently been made to reintroduce this species.

Powell, R. A. 1981. *Martes pennanti.* Mammalian Species 156:1–6.

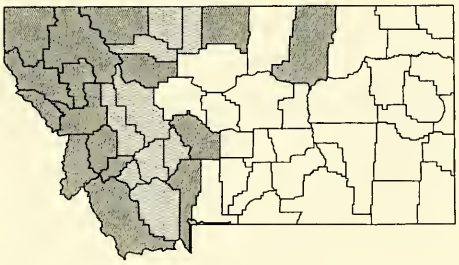
Short-tailed Weasel
Mustela erminea



Short-tailed weasel (*Mustela erminea*).

Scientific Name: The short-tailed weasel was first described by Carolus Linnaeus, in 1758, from specimens obtained in Sweden. Specimens were first collected and described from North America in 1838. The generic designation *Mustela* is the Latin term for "weasel." The specific epithet *erminea* is from the Old French word "ermine," which refers to the white winter color of this species.

Description: The short-tailed weasel is 1 of the smallest mustelids in Montana. Only the least weasel is smaller. The short-tailed weasel has the classic "weasel" shape, with a long fuselage-shaped body; long neck; prominent tail (although shorter than the long-tailed weasel and hence the vernacular name); small, rounded ears; and short legs. Dorsal coat color is reddish-brown to chocolate in summer with a creamy-white venter and black-tipped tail. Winter color is white with black-tipped tail. At a distance, the short-tailed weasel may



Map 92. Distribution of the short-tailed weasel, *Mustela erminea*.

be confused with 2 other Montana weasels, the least weasel and the long-tailed weasel. The short-tailed weasel is larger than the least weasel and has a longer tail, with a black tip. The long-tailed weasel has a yellowish–orangish venter in summer rather than the white venter of the short-tailed weasel. Specific skull measurements are also useful in species identification (Foresman 2001).

Measurements: [mm(*n*)]: TL = ♂ 290.5(10)/♀ 250.3(4); Ta = ♂ 81.3(10)/♀ 65.8(4); HF = ♂ 36.5(9)/♀ 30.8(4); E = ♂ 14.6(4)/♀ 12.5(2); M [g(*n*)] = ♂ 116.2(10)/♀ 71.8(2). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: The short-tailed weasel is a holarctic species; in North America, it is distributed from Alaska to Nova Scotia with 2 southward extensions. One covers the western one-third of the continental United States to New Mexico, and the other covers the northeastern half of the United States from the central Dakotas to Iowa, and northern Illinois across to northeastern Kentucky, and the east coast.

Ecology and Behavior: The short-tailed weasel lives in diverse habitats throughout its circumpolar distribution. It is most abundant in montane coniferous forests, particularly along edges and forests in early to mid-successional stages of development. The short-tailed weasel is common in riparian areas and meadow marshes, and occupies a wide elevational gradient in Montana from valley bottoms to alpine slopes. It is particularly adapted to regions with heavy snows, as it can feed on small mammals in the subnivean space.

Most den sites are in hollow trees or rock outcrops. Nests and burrow systems of voles may also be used. Typically, the nest is lined with grass, leaves, and the fur of rodents that have been eaten. The short-tailed weasel is an efficient predator of small mammals especially voles. The meadow vole is its primary food source, although animals as large as chipmunks, pikas, and rabbits (the mountain cottontail in Montana) also may be taken. Birds, amphibians, reptiles, and insects may also be eaten if small mammals are scarce.

When foraging, the short-tailed weasel is constantly on the move running through rock crevices and along vole runways in search of prey. When individuals search for pikas in alpine boulder fields; they move rapidly, keeping their body quite straight as they glide over the rocks. When prey is spotted the short-tailed weasel attacks with amazing speed and kills with a bite to the base of the head. Activity is spaced at 3- to 5-hour intervals throughout the 24-hour period interspersed with rest periods. During favorable weather, short-tailed weasels are more active than during rain or severe cold. Foraging during winter occurs under the snow, in the subnivean space, where rodent activity continues. The short-tailed weasel is particularly adept at moving through snow tunnels as its body size is not much larger than the voles it prefers. Resource partitioning between sympatric short- and long-tailed weasels occurs during winter. The larger long-tailed weasel is too big for the subnivean tunnels of *Microtus* and thus catches rabbits and hares on the surface of the snow. When voles are abundant, short-tailed weasels will kill and cache them for later use.

The short-tailed weasel is solitary. Males and females only associate during the breeding season in the spring. Males have larger home ranges (typically 10–40 ha) which may overlap those of several females.

There is little overlap between home ranges of individuals of the same sex. Territories, marked with secretions from anal scent glands, are aggressively defended. An individual may travel several kilometers a day in search of food, depending on prey abundance.

Molts occur spring and autumn. The autumn molt produces a coat of white in preparation for winter. The only other mustelid in Montana with such a color transformation is the long-tailed weasel. Populations of short-tailed weasel in more southern localities do not turn white, although they do molt into a denser winter coat. The color change is controlled by ambient temperatures to which the animal is exposed. Pigment production (melanin) responsible for brown color is under the control of the pituitary hormone melanocyte-stimulating hormone (MSH). Synthesis and secretion of this hormone is under temperature control in short-tailed and long-tailed weasels; cold temperatures inhibit it's production while warm temperatures allow it. Thus, in autumn as ambient temperatures decrease, MSH production declines. Melanocytes are not stimulated to produce melanin and the newly forming hairs lack pigment and thus appear white. In spring, as temperatures rise, MSH increases, and stimulates melanocytes to produce pigment coloring the new hair brown. By becoming white when the environment changes to white, both short-tailed weasel and long-tailed weasels have effective camouflage.

Because in winter short-tailed weasels rely on voles that only live in the tight subnivean spaces, short-tailed weasels cannot deposit layers of fat on their frame nor produce a thick, bulky, winter coat. Thus the short-tailed weasel must live in a well insulated nest cavity and adjust its activity.

Reproduction: Breeding in Montana occurs in May and June. Gestation is 10 months long and includes a 9 month delay of implantation. Parturition occurs in March and April and females exhibit a postpartum estrus. Litter sizes range from 4–13, although litters of 4–8 are most common. Lactation continues for 7–12 weeks but young begin experimenting with solid food after 4–5 weeks. Females reach adult body size at 6 months whereas males attain adult size at 1 year. Age at sexual maturity is also sex specific. Female short-tailed weasels are 1 of the most precocious carnivore species. Young conceive before they are weaned, some even before their eyes open at 4–6 weeks. Males do not reach sexual maturity until their 1st year.

Status: Common; classified as a furbearer. Trapping records do not differentiate between short-tailed and long-tailed weasels; 343 individuals were collected in 1995.

King, C. M. 1983. *Mustela erminea.* Mammalian Species 195:1–8.

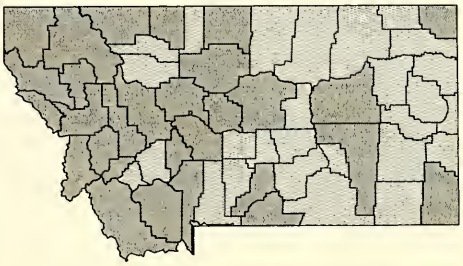
Long-tailed weasel
Mustela frenata

Long-tailed Weasel (*Mustela frenata*).

Scientific Name: The long-tailed weasel was first described by Lichtenstein, in 1831, from type specimens collected in Ciudad Mexico, Mexico. The name applied then is still used today. Meriwether Lewis and William Clark had earlier obtained a specimen during their stay at Fort Mandan on 9 November 1804 (Moulton 1987a). They shipped it to Thomas Jefferson and, although detailed descriptions made by Lewis in 1804 provided the 1st scientific discussion of this species, these were never published. The generic designation *Mustela* is the Latin word for "weasel." The specific epithet *frenata* is from the Latin frenum, meaning "bridle," an apparent reference to the white face markings found on some individuals.

Description: As the vernacular name suggests, the long-tailed weasel has a long tail, longer than any other North American weasel. In fact, the tail is >44% of the length of head and body. The long-tailed weasel has the typical "weasel" shape with a elongated body, short legs, narrow head, and small, rounded ears. Body color is distinct from other members of the genus. Summer pelage is pale to dark brown dorsally and yellowish on the venter with a black-tipped tail. The long-tailed weasel molts in autumn to a white pelage which retains the black-tipped tail. Southern populations may not change color in winter. Males are often 10%–20% longer in total body length and nearly twice as heavy as females. Of the 3 weasels in Montana, the long-tailed weasel can be separated from the least and short-tailed weasels by its longer tail. Because of the extreme sexual dimorphism seen in these species, small female long-tailed weasels may approach the size of large male short-tailed weasels. Coat color differences will distinguish between these individuals however. The yellowish venter separates the long-tailed weasel from both other forms.

Measurements: [mm(*n*)]: TL = ♂ 420.5(10)/♀ 336.0(3); Ta = ♂ 143.5(10)/♀ 111.7(3); HF = ♂ 46.7(10)/♀ 38.0(3); E = ♂ 24.8(4)/♀ none; M [g(*n*)] = ♂ 260.7(10)/♀ 168.0(2). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.



Map 93. Distribution of the long-tailed weasel, *Mustela frenata*.

Distribution: The long-tailed weasel is distributed widely across North America from the Canadian provinces of British Columbia, Alberta, and Saskatchewan across the remaining southern extremes of Canada, throughout the continental United States, Mexico, Central America, and into portions of northern South America.

Ecology and Behavior: The long-tailed weasel uses a wide variety of habitats. From the dense forests of western and southcentral Montana to the arid enclaves of the southeast, including densely forested stands at high elevations, in Missoula County in the west, and the arid deserts of the Pryor Mountains of southcentral Montana. Usually the long-tailed weasel prefers open habitats, particularly grasslands and forest edges with patchy resources. Fencerows along cultivated wheat fields are ideal locations for the long-tailed weasels to forage.

As with the short-tailed weasel, long-tailed weasels use rock outcroppings for den sites and dens of ground squirrels or other species. The nest chamber is often lined with grasses and the fur of prey species. Foraging occurs during the night although weasels may be observed at any hour. Small mammals are the primary prey species, with voles (particularly the meadow vole), mice (especially deer mice), chipmunks, ground

squirrels, and even rabbits and hares fair game. The larger species are taken by males because of their larger body size. In captivity long-tailed weasels ate 4–6 mice daily, but would kill as many as they were given, caching the remainder for later use. Captive individuals eat 18%–40% of their body weight daily.

When prey are abundant, home ranges may average 10 to 20 ha, but range size may expand to ≥100 ha when prey are scarce. Typical foraging extends over a wide area, with the animal constantly on the move checking out crevices, brush piles, and burrows for prey. The animal's sense of smell is probably used to direct its movements, and once it picks up a fresh scent it is tenacious in pursuit. During winter, long-tailed weasels hunt red-backed voles in tree wells where less snow is present. As with other mustelids, the long-tailed weasel kills its prey by biting at the base of the neck.

During their expedition through the northwest in 1804, Lewis and Clark obtained many specimens of the long-tailed weasel (misidentified as an "ermine"), from the Shoshoni, in the form of a garment, termed a "tippet," which was worn like a cloak. Lewis remarked that:

> "... they are no doubt extreemly plenty and readily taken, from the number of these tippets which I have seen among these people and the great number of skins employed in the construction of eact timppet. scarcely any of them have employed less than one hundred of these skins in their formation." (Moulton 1988:128).

Reproduction: Testicular recrudescence occurs in April and active spermatogenesis continues through August. Although males can breed throughout this 5 month period, females do not come into estrus until late July thus the peak of the breeding season in western Montana occurs then. Breeding will extend into August. Gestation is 9 months in length including an 8 month delay in implantation. Parturition occurs in April and litter size averages 6–9.

Male and female littermates mature at different rates. Males approach, but do not attain, adult body weight before their 1st winter, by day 80. Sexual maturity is not reached until the 2nd summer. Females grow much more rapidly, reaching sexual maturity within 3 months and breeding. Unlike the short-tailed weasel, female long-tailed weasels do not have a post-partum estrus; instead, mating occurs after lactation has ended in July.

Status: Common; classified as a furbearer. In 1995, 343 animals were collected (some of these may have been short-tailed weasels as no distinction in made by Montana Fish, Wildlife and Parks).

Sheffield, S. R., and H. H. Thomas. 1997. *Mustela frenata.* Mammalian Species 570:1–9.

Black-footed Ferret
Mustela nigripes

Black-footed ferret (*Mustela nigripes*). See plate 11.

Scientific Name: The black-footed ferret was first described by John James Audubon and John Bachman, 2 of America's most preeminent naturalists, in 1851, from a specimen taken along the Platte River in Nebraska by A. Culbertson. This specimen was subsequently traded through Fort Laramie, Goshen County, Wyoming which is described now as the type locality. Originally identified as *Putorius nigripes,* the generic designation *Mustela* (Latin for "weasel") was assigned by Miller, in 1912. The specific epithet *nigripes* is a composite of the Latin niger (nigr-) which means "black" and pes which means "foot."

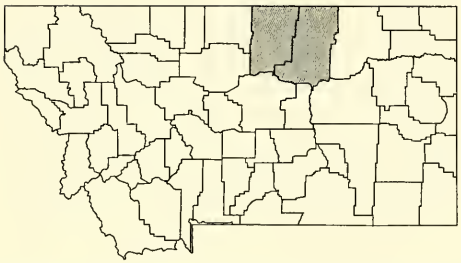
Description: The black-footed ferret exemplifies the typical "weasel" body form, with an extremely long torso, short fore- and hindlegs, and a long tail. It is about the size of the mink, but differs in color. Body color is a yellowish-buff, although parts of the face and belly are whitish. Its feet are black as is the tip of its tail. Most distinctive is the black mask covering its eyes. The black-footed ferret does not turn white in winter. The black-footed ferret should not be confused easily with any other wild Montana mustelid. Its distinctive color and habitat association separates it from the similarly sized mink. Although long-tailed weasels have been mistaken for black-footed ferrets, the black mask and feet clearly distinguish the 2 species. The European polecat, *Mustela furo,* which is now sold as a pet in the United States, is more similar in size and appearance, but it would not be found in the wild.

Measurements: [mm(*n*); Hall 1981]: TL = ♂ 500–533; Ta = ♂ 114–127; HF = ♂ 60–73; E = ♂ 29–31; (females 10% smaller); M [g(*n*)] = ♂ 1,104(8)/♀ 723(10). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: Black-footed ferrets originally inhabited a majority of the Great Plains and semiarid grasslands from southern Alberta and Saskatchewan through a swath encompassing Montana and North Dakota to Arizona, New Mexico, and the northern one-third of Texas. By the early 1900s, its population was declining due to the eradication of prairie dog colonies, its primary prey base. By 1987 the black-footed ferret was on the verge of extinction, and considerable federal efforts were begun to develop a captive breeding program (Clark 1989). Through these efforts, black-footed ferrets now are in Wyoming and South Dakota, and have been reintroduced into Phillips County in northcentral Montana.

Ecology and Behavior: The black-footed ferret is tightly associated with grassland habitats primarily because of its extreme dependence on prairie dogs for food. Historically, its population numbered >1 million individuals and was tied to colonies of black-tailed, white-tailed, and Gunnison's prairie dogs. Ferrets do not dig their own burrows, but rather use those of prairie dogs and occasionally those of ground squirrels or marmots (Fig. 68).

Although prairie dogs may be the over-



Map 94. Distribution of the black-footed ferret, *Mustela nigripes.*

Fig. 68. Black-footed ferret exiting a prairie-dog burrow.

whelmingly preferred prey species (found in 87–91% of all scats), ferrets will eat deer mice, meadow voles, sagebrush voles, white-tailed jackrabbits, and mountain cottontails.

The black-footed ferret is primarily nocturnal, becoming active just after sunset. In winter, activity occurs most often after dusk; in summer, activity is bimodal with a peak between 0330 and 0400 hours (Clark 1989). Animals have been observed above ground during severe snow storms, and at temperatures as low as −39°C (Clark 1989).

Home ranges are 40–60 ha (Forrest et al. 1985). Individuals remain at 1 prairie dog colony as long as prey are available. One female and 4 young occupied 12 different prairie dog burrows in the same colony over 2 months (Sheets et al. 1972). In autumn, juveniles may disperse over long distances, moving 2–3 km to adjacent prairie dog towns.

With the westward growth of the United States in the early 1900s, substantial federal programs were established in an effort to eradicate prairie dog colonies so that agricultural crops could be expanded. Between 1912 and 1923 nearly 160,000 gallons of strychnine-soaked grain were distributed throughout Colorado alone! More than 31 million prairie dogs may have died in these efforts (Clark 1989). Not only did such efforts destroy the primary prey base for the ferret but many ferrets themselves probably fell victim to these poisons. By 1985 all remaining wild ferrets, totaling 12 individuals, were captured and held for breeding. This remarkably small nucleus produced several hundred offspring which are now being reintroduced in several states. Recently some physical abnormalities have appeared in offspring from captive bred individuals as a result of continued inbreeding.

The last known wild record of a black-footed ferret in Montana was in 1953; this specimen was found dead along the highway north of Alzada in Carter County (Hoffmann et al. 1969). Additional specimens were previously obtained from Carter County (near Piniele, 1944), Rosebud County (near Ingomar, 1952), Golden County (near Lavina, 1948), and Yellowstone County (near Billings, 1949). Reintroduction efforts in the state began in the autumn of 1994 when 35 animals were released on the UL Bend National Wildlife Refuge in south Phillips County. Subsequent releases have occurred yearly totaling an additional 136 individuals through autumn 1999 [M. R. Matchett, pers. comm.]. Spring 2000 surveys identified 31 ferrets of which 27 were wildborn at UL Bend, 20 born just the previous year. This indicates a high [53%] overwinter survival of wildborn kits. Since 1997, 153 individuals (13 adults and 140 kits) were released on Fort

Belknap Indian Reservation in northern Blaine and Phillips counties [M. R. Matchett pers. comm.].

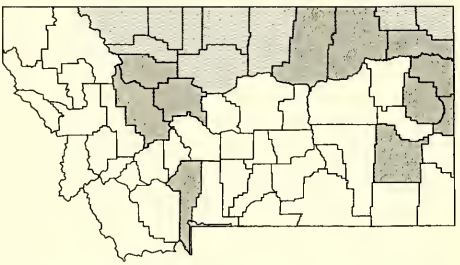
Reproduction: The black-footed ferret does not delay implantation. Breeding begins mid-to-late March and may extend into late April. Parturition occurs in late April to May after a 42–45 day gestation period. Litter sizes average 3–5. Young have been first observed above ground in July, dispersing by September. Sexual maturity is reached by 9 months.

Status: Although reintroduction efforts have begun, the black-footed ferret remains on the federal endangered species list.

Hillman, C. N., and T. W. Clark. 1980. *Mustela nigripes.* Mammalian Species 126:1–3.

Least Weasel
Mustela nivalis

Scientific Name: The least weasel was not recognized by science nor officially described until 1896, when Bangs proposed the name *Putorius rixosus* for the type specimen obtained from Osler, Saskatchewan. The current name, *Mustela nivalis,* was not accepted until 1958. For much of the early 1900s, the least weasel was identified as *Mustela rixosa,* but cranial morphology led Reichstein to conclude that the European mouse weasel (*M. nivalis*) and the North American least weasel were conspecific; a view held today. The generic designation *Mustela* is Latin for "weasel;" the species name *nivalis* is from the Latin combination niv- which means "snow" and -alis, a suffix meaning "pertaining to;" "pertaining to snow," a reference to its white winter pelage.



Map 95. Distribution of the least weasel, *Mustela nivalis.*

Description: As the vernacular name implies, the least weasel is the smallest of mustelids, and actually the smallest carnivore in the world. It has the elongate body form typical of the weasel family but lacks a long tail. The German term for the least weasel is "mauswiesel," or mouse-weasel, an apt name as the least weasel is no larger than many mice. Body color is a shiny chocolate-brown dorsally with a white throat and venter. The tail is entirely brown. Throughout its more northern distribution, including Montana, the least weasel develops a white coat in winter; more southerly populations may not. Males are 30% larger than females. The least weasel should not be confused with any other Montana mustelid. Its diminutive size and lack of black-tipped tail separates it from both the short-tailed and long-tailed weasels. If only a fleeting observation is made, the least weasel could be mistaken for a vole!

Measurements: [mm(*n*)]: TL = ♂ 178.0(3)/♀ 175.7(7); Ta = ♂ 28.0(3)/♀ 28.0(7); HF = ♂ 22.3(3)/♀ 20.3(7); E = ♂ 11.0(3)/♀ 11.7(3); M [g(*n*); ♀ measurements from Smith 1993] = ♂ 25.3(2)/♀ 29.5(6). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: The least weasel has a holarctic distribution; in North America, it extends from the Canadian provinces reaching a southerly line from Kansas to Virginia, dipping further southward into Georgia.

Ecology and Behavior: Because of its small size, relatively infrequent capture, and nocturnal nature the least weasel is not often seen. Preferred habitats are more open forests, old fields, and grasslands where activity centers along fencerows. It also inhabits open tundra. Most specimens are from northeastern counties in Montana although several records are from the westcentral region, and 1 questionable record was from Gallatin County. Nests are in abandoned chipmunk or vole burrows and are constructed of dry grasses (possibly formed by the previous occupants) and lined with the fur of prey. The entrances to burrows are $\leq$2.5 cm in size.

The least weasel feeds predominantly on small mammals such as red-backed voles, deer mice, prairie voles, and harvest mice. Because of its small size and concomitant high metabolic rate, it has an intermittent feeding strategy which continues day and night. On average 1–2 g of food are eaten/hour, or about 1.3 mice/day. Total consumption/feeding bout is limited to a few grams necessitating 5–10 feedings a day. The least weasel forages opportunistically attacking all prey offered, as is appropriate for a small carnivore with high metabolic demands. However, capture success is a function of prey size and prey aggressiveness. Small rodents such as adult white-footed mice or juvenile meadow voles, weighing between 14 and 30 g, are readily taken. Larger, adult meadow voles ranging from 45–80 g are avoided. Thus medium-sized prey are selectively attacked even when larger species are abundant. Food caches are made and repeatedly visited.

Least weasels are active throughout winter, and depend on the subnivean space for foraging. Where subnivean spaces form, the least weasel can succeed, even in sympatry with the short-tailed weasel, because the least weasel can more effectively use this environment. Snow also provides an important layer of insulation from daily temperature extremes. Least weasels are nocturnal throughout the year, foraging most often after dusk.

Reproduction: Unlike the short- and long-tailed weasels, the least weasel does not delay implantation. Breeding may occur throughout the year even during the coldest months of winter. It can produce 2 or more litters/year of from 1–6 young ($\bar{x}$ = 4.8) following a gestation of 35 days. As with other small species, rapid growth occurs following birth, with adult weights attained within 12–15 weeks. Weaning occurs by 6–7 weeks of age. Females attain sexual maturity by 4 months of age, males by 8 months.

Status: Rare.

Sheffield, S. R., and C. M. King. 1994. *Mustela nivalis*. Mammalian Species 454:1–10.

Mink
Mustela vison

Mink (*Mustela vison*).

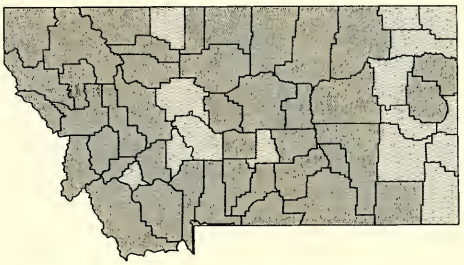
Scientific Name: The mink was first described by Schreber, in 1777, from a type specimen obtained in eastern Canada (present day Quebec). The scientific name applied at this time is still in use today. The generic designation *Mustela* is Latin for "weasel;" the specific epithet *vison* is of either Icelandic or Swedish origin, a term also meaning "marten or weasel." The common vernacular is thought to have originated from the Swedish word maenk.

Description: The mink shares the elongated body form of the mustelid family, although it is more stout than weasels, with a long tail and short legs. Its pelage is much more luxuriant than weasels (a function of its semi-aquatic nature) and is a dark chocolate in color with variable white patch(es) along its throat or belly. Ears are rounded and small and its feet are partially webbed. In Montana, males can be nearly twice as large as females. The mink is considerably larger than all 3 weasels in Montana and much darker in color, thus it should not be confused easily with these. However, in body size and stature it closely resembles the American marten. But the mink has a much darker color and white ventral markings (compared to the American marten which is a lighter brown with a yellow-orange throat patch). Ear shape can also be used to distinguish these species. Although somewhat similar in body size to the black-footed ferret, color differences and habitat preferences preclude confusion.

Measurements: [mm(*n*)]: TL = ♂ 591.5(4)/♀ 457.0(2); Ta = ♂ 190.3(4)/♀ 134.0(2); HF = ♂ 69.0(4)/♀ 51.0(2); E = ♂ 22.0(2)/♀ 20.0(2); M [g(*n*)] = ♂ 1,098.4(4)/♀ 446.5(2). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: Mink are widely distributed across North America from Alaska across all Canadian provinces to central California in the west and Florida in the east. In the southwest, they enter the northern regions of Nevada, Utah, and New Mexico before dipping southward across Texas. Arizona is the only state without mink.

Ecology and Behavior: The mink is semi-aquatic and thus is tightly associated with riparian zones. In Montana, it frequents a variety of habitats from the dense coniferous forests of the west to the more open grasslands and even semi-deserts of the east and south, as long as water is available. Dens are located in log or rock piles, often close to ponds, streams, or marshes.



Map 96. Distribution of the mink, *Mustela vison*.

Muskrat dens are used as well, often after the occupants are eaten. These dens have several entrances. Nests are constructed of leaves, grass, and the fur and feathers of prey.

Mink, like other mustelids, remain active all year, foraging primarily at night. Frequent activity may also occur at dawn or dusk. Because of its semi-aquatic nature, terrestrial mammals such as voles, mice, and rabbits are routinely caught, as are aquatic forms such as muskrat. Fish and crayfish are heavily used particularly during winter. In open prairie habitats, waterfowl may make up over 50% of the diet, and other birds including grebes and coots may be taken. Food is most often taken back to the den for consumption.

Mink are not social, preferring to live alone except during the breeding season although home ranges may overlap. Males range more widely than females. Home range size is a function of habitat quality. Along the Madison River males may travel up to 4.9 km across their home range. Minimum home ranges for 2 females were 7.8 and 20.4 ha. Males from a wetland in Manitoba had an average home range of 6.5 km^2. Traveling from one end of a home range this large to the other end may require several days, and animals will shelter in dens throughout their home range. Populations may be locally abundant. One 33.6 km^2 area near Three Forks, Montana, had 280 individuals.

The dense winter underfur of mink greatly enhances the trapping of air and provides increased insulation. During winter, forag-

ing in water is limited to pursuit of prey after detection from above water. Retention of an air layer, shunting of blood away from the surface, and elevated metabolic heat production all help to maintain the animal's core body temperature during foraging.

Mink have been trapped for nearly 200 years because of the quality of their pelts. Commercial mink farms are still widely found throughout the United States, with several in Montana. Such operations often selectively breed and raise more than 10,000 animals/year, adjusting the pelt color of their stock to accommodate the commercial market. Most fur raised in this country supplies the European market.

Reproduction: In Montana, breeding extends from late February through early April with a peak in March. The length of gestation varies: without a delay in implantation gestation lasts 40 days, but this may be extended to about 75 days if a delay occurs. The variation is influenced by temperature, photoperiod, and the date of mating. Females often mate again with a different male 6–8 days after their 1st mating and the subsequent litter produced will have been sired by 2 males. A single litter is produced in April or early May. Litter sizes average 3–5. Offspring mature quickly and are weaned at 5–6 weeks. Sexual maturity is reached the following spring at 10 months.

Status: Common and locally abundant; classified as a furbearer. Even with a reduced fur market, over 900 animals are harvested each year.

Larivière, S. 1999. *Mustela vison.* Mammalian Species 608:1–9.

Badger
Taxidea taxus

Badger (*Taxidea taxus*).

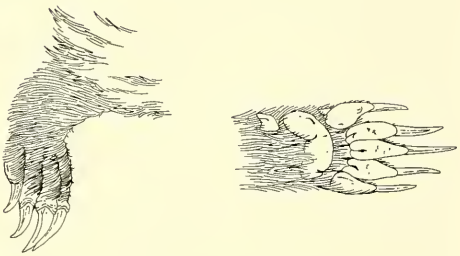
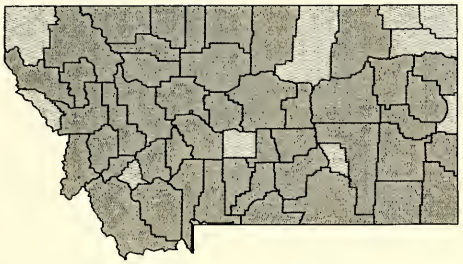


Fig. 69. Claws of badger modified for digging.

Scientific Name: The badger was first described by Schreber, in 1778, from a specimen obtained southwest of Hudson Bay, in what is today Ontario. The original name, *Ursus taxus,* which is Latin and New Latin for "bear badger," illustrates the earliest held belief that badgers were closely related to the bears. The scientific name used today, *Taxidea taxus,* was first suggested in 1894, by Rhoads. The generic name *Taxidea* has both Latin and Greek origins, taxus meaning "badger," and eidos meaning "like," "badger-like;" the specific epithet, *taxus,* is New Latin for "badger" as well.

Description: Built like no other mustelid, the badger is remarkable for its greatly accentuated, dorsal-ventrally flattened stature, its extremely short and robust legs, and its massive curved foreclaws (Fig. 69). Head is triangular in shape, and ears are rounded. The rough pelage lacks the dense underfur of terrestrial mustelids and is a mixture of gray, brown, and black hairs giving an over-



Map 97. Distribution of the badger, *Taxidea taxus.*

all mottled appearance. A distinctive white stripe starts on the nose and continues down the forehead to the middle of the shoulders. Other facial markings include large black cheek patches bordered anteriorly by white fur. The tail is about one-fifth of total body length and is bushy. All these characteristics reflect a semi-fossorial existence. The badger should not be confused with any other Montana mammal. Its large body size and morphological characteristics related to its semi-fossorial nature, along with its distinctive markings, make it easily recognizable.

Measurements: [mm(*n*)]: TL = ♂ 746.0(6)/♀ 718.5(4); Ta = ♂ 138.3(6)/♀ 129.7(3); HF = ♂ 101.0(6)/♀ 105.0(2); E = ♂ 41.5(4)/♀ none; M [kg(*n*)] = ♂ 7.4(5)/♀ 6.5(6). Dental formula: i 3/3, c 1/1, p 3/3, m 1/2, total 34.

Distribution: The badger is widely distributed from central British Columbia across the Canadian provinces to southern Ontario, Michigan and Ohio, southwestward across Missouri, Oklahoma, and Texas into central Mexico and west to the Pacific coast.

Ecology and Behavior: Although distributed widely across North America, the badger is tied to grassland communities and in particular to open plains and shrub-steppe habitats. An environment dominated by big sagebrush, bluegrass, and cheatgrass provides the prey base (notably ground squirrels) for badger. Badgers dig their own dens, often constructing new dens almost daily throughout the summer as they forage. Females move several times during spring and summer months, using many maternal dens (Linzey 1978). This behavior may be due to the accumulation of feces in the den or the need to move to more productive feeding grounds. Maternal burrows may be >9 m in length and end in a nest chamber 1 m underground, lined in grass. As autumn approaches, fewer dens are used, and by winter a single den is maintained. Previous dens may be revisited often during foraging, as badger dens may be taken over by badger prey (Linzey 1978; Messick and Hornocker 1981).

The badger has evolved behaviorally, physiologically, and morphologically in concert with its fossorial prey base to such a degree that many consider it to be 1 of the most highly specialized, extant carnivores. Powerful forefeet supporting claws over 2.5 cm in length, webbing between the toes, extreme body musculature, and loose, thick skin covered by coarse hair allow this animal to dig its way underground in just a few minutes. It can easily dig faster than fleeing prey. An exclusive carnivore, badgers eat ground squirrels, cottontails, jackrabbits, pocket gophers, prairie dogs, as well as numerous reptiles and insects (Messick and Hornocker 1981). Seasonal trends occur based on prey availability. Badgers spend long periods underground during the coldest winter months and will undergo torpor. A 50% reduction in heart rate and a 9°C reduction in core body temperatures occurred during a 29-hour torpor cycle (Harlow 1981). Repeated torpor bouts occurred over >70 days spent below ground.

Badgers are active predominantly at night. Home ranges vary according to habitat and food availability. On the Snake River Birds of Prey Natural Area in southwestern Idaho home ranges varied from 0.4–3.8 km^2 for females to 0.8–3.4 km^2 for males (Messick and Hornocker 1981); home ranges 1.5–2.5 times this size occurred in Utah (Linzey 1978). Although solitary, badgers maintain overlapping home ranges both between sexes and age groupings.

Reproduction: Testicular recrudescence begins in May, with full development from June to August. In Montana, most mating occurs between August and September. An obligate delay of implantation lasts for 6.5 months, with implantation in February. Post-implantation development lasts about 1.5 months with birth in March to early April. Litter sizes average 2–3; young are weaned by June and grow rapidly. Females may breed at 4 months of age, although males are not reproductively mature until their 2nd year.

Badger are relatively long-lived; captive animals have lived for over 15 years.

Status: Common; classified as a furbearer. Nearly 500 individuals were trapped in 1995.

Long, C. A. 1973. *Taxidea taxus.* Mammalian Species 26:1–4.

Family Procyonidae—Raccoons*

Raccoon

Procyon lotor

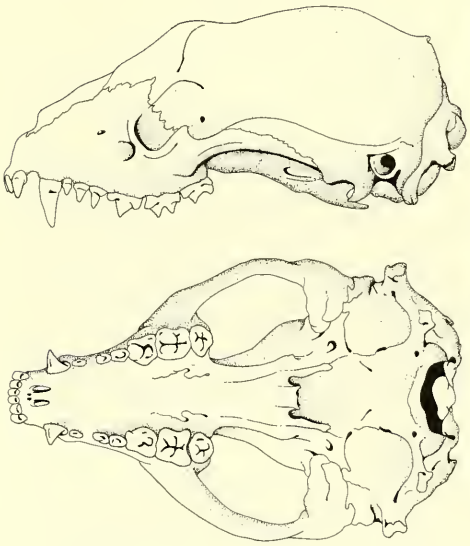


Fig. 70. Skull of a raccoon (*Procyon*).

Raccoon (*Procyon lotor*). See plate 12.

Scientific Name: The raccoon was 1st described by Carolus Linneaus, in 1758, from a type specimen obtained in Pennsylvania. Originally identified as *Ursus lotor* (reflecting its physical appearance and believed relatedness to a bear), this species was reassigned to the genus *Procyon* by G. C. C. Storr, in 1780. The generic distinction *Procyon* is a Greek combination, the prefix pro- meaning "before" and the word kyon meaning "like a dog," an origin not clearly understood. The specific epithet *lotor* is

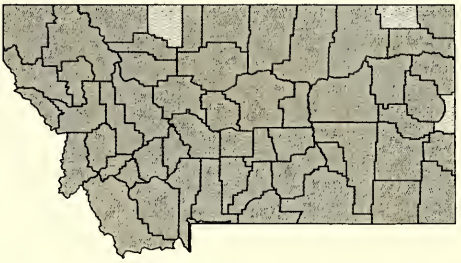
* For representative skull characteristics of this taxonomic family refer to Fig. 70.

New Latin for "a washer," referring to its perceived habit of washing its food before eating.

Description: The raccoon is a medium-sized carnivore with distinctive markings, most notably the sharp black mask surrounded by white nose and eyebrows and the 5–7 brown–black tail rings alternating with lighter hairs. Other than these markings, the pelage has a grizzled appearance of predominant grayish to blackish color. Ears are small and rounded, and feet have fine, unwebbed toes with well-developed, although small, non-retractable claws. The gait is semi-plantigrade to plantigrade producing a shuffling motion. Raccoons should not be confused with any other Montana mammal. Its distinctive "bandit" mask and tail rings are clear identifying characteristics.

Measurements: [mm(n)]: TL = ♂ 836.4(6)/♀ 743.1(4); Ta = ♂ 259.8(6)/♀ 214.8(3); HF = ♂ 120.2(6)/♀ 117.8(3); E = ♂ 62.3(6)/♀ 53.0(2); M [kg(n)] = ♂ 7.1(7)/♀ 5.4(5). Dental formula: i 3/3, c 1/1, p 4/4, m 2/2, total 40.

Distribution: Raccoons are widely distributed across North America, from the southern to central Canadian provinces to Panama. It is only absent from a narrow band extending through regions of Nevada, Utah, Wyoming, and Colorado. Although the raccoon has probably been in eastern Montana since historical times, especially along the Yellowstone River and Little Big Horn River valleys, it has expanded its range notably in recent years. Movement from Idaho into the Bitterroot Valley was first noticed in the 1940s and the 1st specimen was collected from Florence (Ravalli County) in 1945 (Hoffmann et al. 1969). Further extensions northward into the Kootenai and eastward into the Flathead Valley occurred in the 1950s and 1960s, as did movement along the Missouri River into more central areas of the state.



Map 98. Distribution of the raccoon, *Procyon lotor*.

Ecology and Behavior: Raccoons occupy a wide variety of habitats throughout Montana, from the densely forested western mountains to the arid grasslands of the east. In the east they are found in rock coulees, wooded draws, upland croplands, and along hardwood riparian zones of the Yellowstone and Missouri Rivers. Den sites, several in number, may occur in rock crevices, abandoned marmot burrows, caves, or hollow trees; resting sites are often in tree brooms. When threatened, raccoons seek refuge in trees. Raccoons forage over a wide area on a wide variety of foods. Foraging begins at sunset and continues throughout the night, with animals retreating to resting dens at sunrise. Home range size is influenced by food and habitat availability. In western Montana where the forests are dense and foods may be locally abundant, home ranges are <50 ha. In the prairies of North Dakota (similar in habitat to eastern Montana) home ranges are huge; average values for males may be >2,500 ha, and those for females >800 ha (Fritzell 1978).

The raccoon is clearly omnivorous and will eat berries and nuts, commercial crops such as corn and orchard fruits, aquatic invertebrates (crayfish, snails, and clams), fish, birds, small mammals, and insects. Predation by raccoons on waterfowl, their eggs, and nestlings, may account for significant mortality on refuges such as Ninepipe National Wildlife Refuge in western Montana.

Raccoons may "wash" its food before it eats it although the behavior may also serve to identify various parts of prey, such as the

claws of crayfish; 4 digits are highly dexterous and finger activity occurs even when no food is being manipulated.

Raccoons do not have a strong social structure, but will accommodate one another, and move together when visiting locally abundant food sources. Groups of 2 to 3 adults traveling together may displace single individuals while foraging; agonistic displays are short-lived.

Individuals most often den singly during summer and autumn, but may share dens in winter. In fact, 23 individuals (12 ♀, 10 ♂, 1 unknown), over half of which were juveniles, shared the cellar of an abandoned house. Sharing dens enhances winter survival by allowing individuals to share body heat. Raccoons do not undergo torpor, and maintain high body temperatures while resting for extended periods during severe cold spells.

Reproduction: Breeding in Montana probably extends from January into late spring. With a gestation of 63 days, parturition may occur from March into early summer. Litter sizes range from 2–5.

Status: Common; classified as a furbearer. Over 4,600 animals were taken in 1995.

Lotze, J-H., and S. Anderson. 1979. *Procyon lotor*. Mammalian Species 119:1–8.

Family Ursidae—Bears*

Black Bear
Ursus americanus

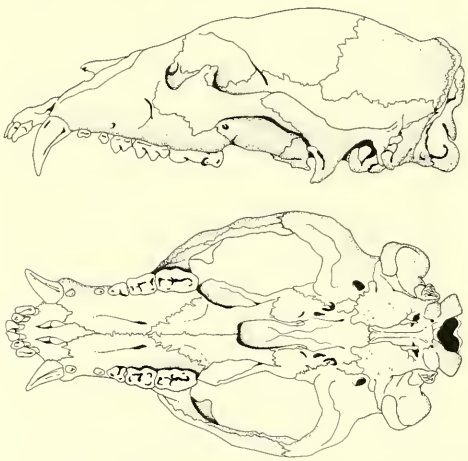


Fig. 71. Skull of a bear (*Ursus*).

Black bear (*Ursus americanus*). See plate 12.

* For representative skull characteristics of this taxonomic family refer to Fig. 71.

Scientific Name: The black bear was first described by Pallas (1780), in 1780, from specimens collected in eastern North America. The original name is still accepted today. The generic distinction *Ursus* is from the Latin ursus meaning "bear." The specific epithet *americanus* is the Latinized form of "America" referring to the type locality.

Description: The black bear is a large-bodied carnivore with a sloping, elongated snout; rounded, erect ears; and short, powerful legs. Fore- and hind feet have 5 toes with non-retractable, curved claws. Tail is short and almost unnoticeable. The fur is dense and luxuriant in winter. Color varies from a dark, glossy black to a reddish-brown or cinnamon in Montana.

The black bear is often confused with the grizzly bear, as they overlap in body size and appearance. However, the profile of the black bear's face is straight from the forehead to the tip of the nose; whereas that of the grizzly bear is slightly concave and much more rounded in frontal aspect. Secondly, the grizzly has a distinct hump between the shoulders which the black bear lacks. Third, the claws of the black bear are noticeably shorter than those of the grizzly and not nearly as curved. The longer front claws of the grizzly bear leave tell-tale impressions as a part of the track image, while those of the black bear do not (Fig. 72a). Fourth, the pads on the front feet of the grizzly bear lie in a nearly straight line while the outer pads (1st and 5th toes) of the black bear lie behind the middle 3 (Fig. 72b). Finally, hairs of the black bear, although variable in color, do not possess the light tipping prominent in the grizzly bear.

Measurements: [cm(*n*); Beecham and Rohlman 1994]: TL = ♂ 142.2(44)/♀ 131.2(12); Ta = ♂/♀ none; HF = ♂/♀ none; E = ♂/♀ none; M [kg(*n*); many weights are estimated by the relationship between total length and chest girth measurements—Kasworm and Manley 1988] = ♂ 95.0(10)/♀ 56.4(7). Dental formula: i 3/3, c 1/1, p 4/4, m 2/3, total 42.

Distribution: The black bear is widely distributed from Alaska across all Canadian provinces, extending along the northern regions of Minnesota, Wisconsin, and Michigan. It lives throughout the Appalachian chain, with extensions into Georgia and Florida. In the western United States, it occurs along the coast from Washington to California, inland through Idaho and Montana, and along a band extending from Wyoming to central Mexico.

Ecology and Behavior: The black bear is a denizen of Montana's coniferous forests. It is active from early spring through late autumn, most often during daylight hours. Most activity occurs in the early morning and early evening (Beecham and Rohlman 1994). More nocturnal activity may occur, however, in early spring and late autumn when days are shorter. Home range varies depending on age, sex, season, and habitat quality. Radiotelemetry in central and northern Idaho suggests average annual home ranges are 147 km^2 for adult males and 32 km^2 for adult females (Beecham and Rohlman 1994). In northwestern Montana, home ranges were 100 km^2 for males and 45 km^2 for females (Thier 1990). Black bears are solitary, but not territorial; home ranges of males and females overlap as do those of the same sex, although animals may avoid one another.

During spring, summer, and early autumn black bears forage, rest, or sleep under fallen logs or within dense brush stands. In October, black bears seek out more permanent housing for the winter. Den sites may be constructed at the base of a hollow tree or under fallen logs, although rock cavities and ground dens excavated into a hillside are also used (Beecham and Rohlman 1994; Jonkel and Cowan 1971) as are tree dens (primarily in grand fir or subalpine fir). Often the den cavity (especially that of pregnant females) is lined with grass or small conifer branches.

The black bear is omnivorous, eating both plants and animals, although most of its diet is of plants. Unlike specialized plant

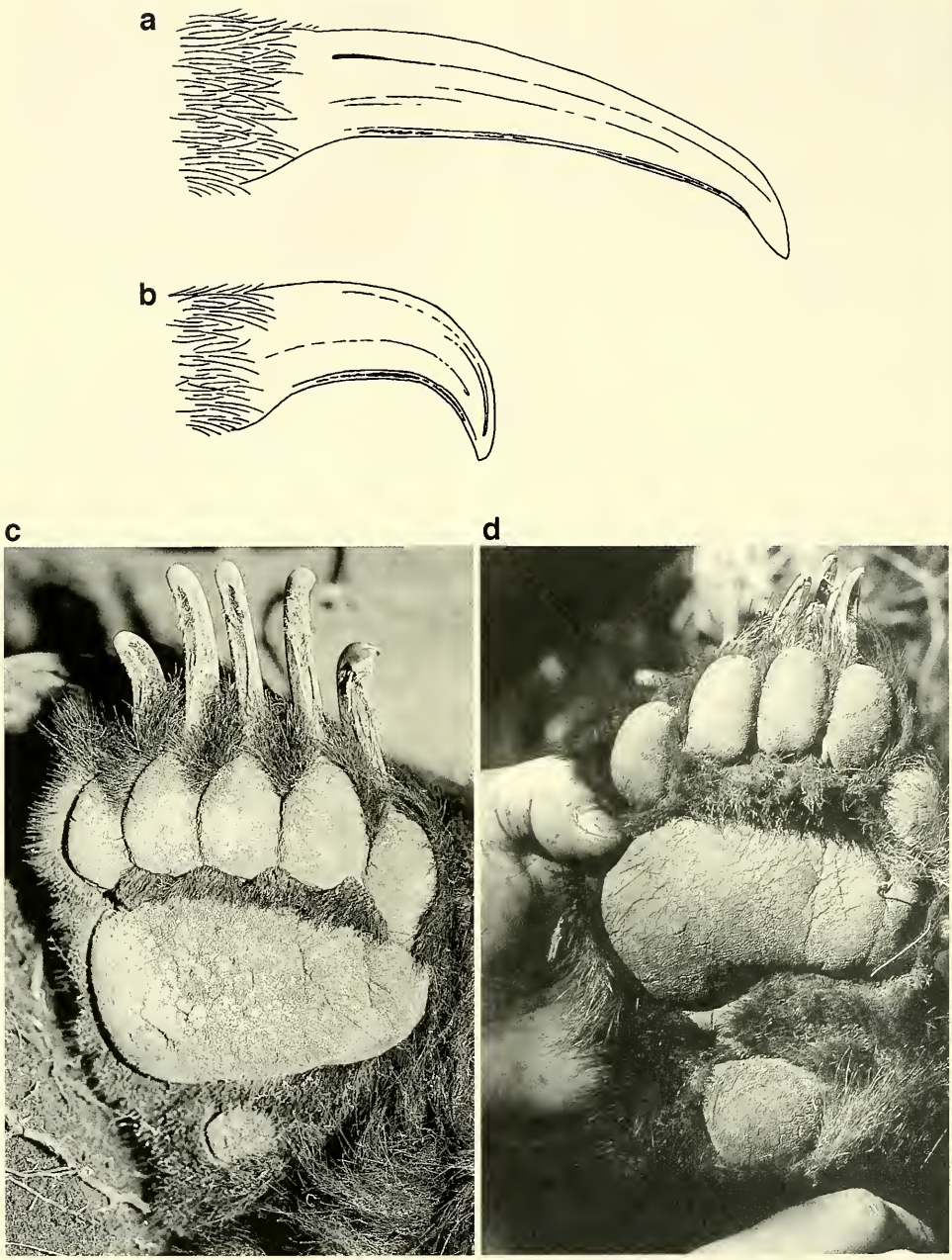
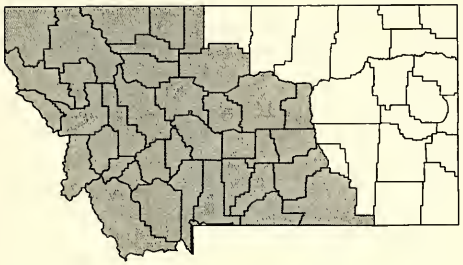


Fig. 72. Claws and foot pads of the grizzly bear (a, c) and black bear (b, d).



Map 99. Distribution of the black bear, *Ursus americanus.*

eaters (herbivores), such as cervids which have a multiple-chambered stomach for rumination of plant materials, or rodents which possess an enlarged caecum where bacterial digestion of cellulose is enhanced, black bears have a simple stomach and lack a caecum. Thus the digestion of leaves and grasses is particularly inefficient. Tremendous amounts of material must be consumed to compensate for this reduced nutritive uptake, a fact which also accounts for the undigested plant material found in their scats. Foraging activity takes advantage of seasonal availability and animals are opportunistic in what they will ingest. In northwestern Montana (Tisch 1961) and Idaho (Beecham and Rohlman 1994) in spring and early summer, newly growing grasses are eaten as well as forbs such as Angelica, cow-parsnip, horsetails, and the flowers of indian paintbrush and dandelions. In July, bears switched their attention to ripening fruits, particularly huckleberries, honeysuckle, and serviceberries, and ate more insects (e.g. ants, bees, grubs), although in good berry years insects were a smaller part of the diet. In autumn, berries and whitebark pine nuts make up the greatest bulk of the diet, although as time went on mountain-ash berries dominated. Mammals are a tiny proportion of the diet, both in terms of volume or frequency of occurrence, during all periods. Small mammals (voles, ground squirrels, and chipmunks, etc.) as well as juvenile cervids (predominantly elk) or cervid carrion are eaten when plant materials are scarce (Jonkel and Cowan 1971; Raine and Kansas 1990).

In late autumn, black bears retreat to their dens to begin a prolonged period of physiological dormancy. They will stop eating or drinking and will not defecate or urinate until several weeks after emerging from their dens in spring. Black bears live off stored body fat and can convert metabolic waste products (primarily the nitrogenous waste urea) into protein (Nelson et al. 1983a). Technically the 3–5°C reduction in body temperature (from an active value of 38°C) and 35% reduction in heart rate (from an active value of 135 bpm) are not great enough to call this dormancy hibernation. These physiological adjustments more accurately reflect entry into a slight torpid condition, termed by some "carnivorean lethargy" (Hock 1960). Regardless, the ability to live for such an extended period of time without eating or drinking, and metabolizing large amounts of fat (estimated at 4,000 calories/day) without urinating or defecating, is truly remarkable (Nelson et al. 1983a).

In Montana, bears emerge mid-April to mid-May depending on weather. Although green vegetation is often not available or abundant yet, black bears need to adjust their digestive systems from the prolonged over-winter shut down and may continue to fast several weeks after emergence.

Reproduction: Breeding begins mid-to-late May and may extend into August in Montana and Idaho (Beecham and Rohlman 1984; Jonkel and Cowan 1971). Females enter estrus in June and will mate several times over 2–4 days. Testicular regression in males begins mid-September (Erickson and Nellor 1964). Pregnant females delay implantation; embryos reach the uterus as blastocysts 1–2 weeks after conception and remain free-floating in there until late November. At this time the embryo implants and renews development, with parturition occurring in late January. Mean litter size is 1.6 (n = 208) in Montana (Jonkel and Cowan 1971; Thier 1990) and

is 1.7 (n = 82) in Idaho (Beecham and Rohlman 1994). At birth, young weigh 225–300 g, their eyes are closed, and they are totally dependent on their mother. Growth is rapid and at emergence from the den young weigh 4.5–9.0 kg (Beecham and Rohlman 1994). Offspring stay with their mother for the 1st full year and disperse during their 2nd summer.

In Idaho females may become sexually mature at 3.5 years, although the average value is 4.9 years (Beecham and Rohlman 1994), similar to the 4.5 years of age for Montana females (Jonkel and Cowan 1971). Conception may be rare at this age. The age at 1st successful reproduction is 6.5 years (Jonkel and Cowan 1971; Thier 1990). Males also reach sexual maturity at 3.5 years, although adult body size is not attained until 6.5 years. Males, like females, probably are not successful breeders until this later age. Age at 1st reproduction is highly dependent on forage quality and abundance. Theoretically, females can breed every other year, and do when food is abundant, but often females go 2 years without breeding and may even skip a 3rd year (Beecham and Rohlman 1994; Jonkel and Cowan 1971).

Status: Common; 1 of Montana's most important game species. In 1995 alone, 51,995 permits were sold (combined archery and gun seasons) and over 900 animals were harvested.

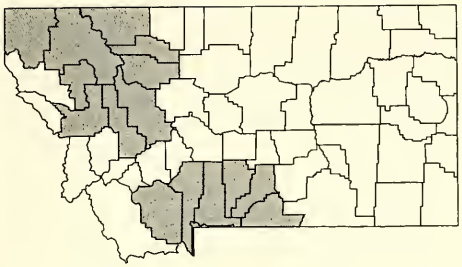
Grizzly Bear
Ursus arctos

Grizzly bear (*Ursus arctos*). See plate 12.

Scientific Name: The grizzly bear was first described by Linnaeus, in 1758, from a specimen obtained in Sweden. In spite of numerous taxonomic revisions over the past 200 years, the initial designation is now accepted for this Holarctic species. The generic distinction *Ursus* is from the Latin meaning "bear." The specific epithet *arctos* is from the Greek arktos also meaning "bear." The term "grizzly" which is applied to North American populations, refers to the grizzled appearance of its pelage. The common name is applied to populations in more inland regions of North America. Along the northwest coast, the term "brown bear" is used, as it is throughout Eurasia.

Description: The grizzly bear is the largest carnivore in Montana. It has a distinctive rounded face with small, rounded ears; small eyes; and a prominent nose. The body is massive and strong, with a noticeable hump between the shoulders; feet are plantigrade with long, curved claws and the tail is small. Color varies greatly in Montana although is usually cinnamon or dark brown, tipped with silver or yellow. Individuals range from nearly blond to black. The grizzly bear may be confused with the more common black bear, however, its distinctive facial features, shoulder hump, and light colored tipping of hair makes identification possible on closer examination. Its longer claws leave a distinct track impression.

Measurements: [cm(n)]: TL = ♂ 188.7(3)/♀ 183.3(4); Ta = ♂/♀ none; HF = ♂ 228.5(2)/♀ 250.5(2); E = ♂/♀ none; M [kg(n); many weights are estimated by the



Map 100. Distribution of the grizzly bear, *Ursus arctos*.

relationship between total length and chest girth measurements—Kasworm and Manley 1988] = ♂ 199.5(8)/♀ 132.3(9). Dental formula: i 3/3, c 1/1, p 4/4, m 2/3, total 42.

Distribution: The grizzly bear inhabits both North America and Eurasia. In North America, it ranges from Alaska, across the Yukon and Northwest Territory, through British Columbia and Alberta. Populations live in 6 disjunct regions of the continental United States in Washington, Idaho, Montana, and Wyoming. Most of Montana individuals live in either Glacier National Park and east of the park along the Canadian border, or in a band encompassing the Mission Mountain range, Swan Valley, Swan Mountain range, and Bob Marshall wilderness. Grizzly bears were reintroduced to the Cabinet Mountains of northwestern Montana.

Ecology and Behavior: Historically, the grizzly bear inhabited most of central and western North America to central Mexico. Forested regions and open grasslands were used. Over the past 100 years its range has been reduced to the more densely forested regions of the northwest (with the exception of the grassland meadows in protected Yellowstone and Glacier National Parks).

Although a carnivore, the grizzly bear is omnivorous and eats numerous plant species in huge quantities. Diet shifts with the season; in spring, when vegetation is lush, grizzly bears forage on grasses, succulents, leaves, flowers and their bulbs, and tubers. Berries, such as the huckleberry, Canada buffalo-berry, strawberry, and kinnikinnick are highly prized and become an important food source as the summer progresses. Insects, grubs, and larvae are eaten abundantly. Concentrations of the army cutworm moth, which estivates on Macdonald Peak in the Mission Mountains in July and August, and ladybird beetles cause as many as 11 bears to congregate to take advantage of this food source. Tell-tale signs of grizzly activity occur in the alpine meadows of Glacier National Park as animals tear up sod looking for invertebrates and tubers. Small mammals such as voles, mice, ground squirrels, and marmots may be eaten as well, although they make up a small portion of the overall diet. Grizzly bears are opportunistic and readily consume carrion. This is the main source of meat in summer and autumn, although old, weak, or diseased ungulates may be captured and killed. Each year a few domestic sheep and cattle are killed as bears confront livestock grazing near forest edges.

Grizzly bears are solitary. Males and females only associate during the breeding season; at other times a female can be found with her cubs, but adult males are absent. Home ranges overlap, with those of several females lying within that of a single male. Females have smaller home ranges, although the size for both sexes is highly variable depending on food and cover, as well as age and social status. Home ranges in the Cabinet–Yaak ecosystem of northwestern Montana are, ♂ 1,290 km^2, ♀ 430 km^2 (Kasworm 1984; 1985); in the Mission Mountains, ♂ 1,398 km^2, ♀ 133 km^2 (Servheen and Lee 1979), and in the Rocky Mountain East Front, ♂ 747 km^2, ♀ 226 km^2 (Schallenberger and Jonkel 1980). Smaller home ranges occur in the North and South Fork drainages of the Flathead River (Mace and Jonkel 1979; 1980).

In late autumn, bears search for a winter den site usually in densely forested areas, on well-drained ground to protect against winter thaws and flooding. In the Mission and Rattlesnake mountains, 41 dens were excavated straight into hillsides (Servheen 1981).

Fig. 73. Typical grizzly bear den (Servheen 1981).

Den sites typically have a slope of between a 28° and 35°, and an aspect consistent with heavy snow depths allowing snow to build up without sliding into the den. A short tunnel leads into a relatively undeveloped main chamber (Fig. 73). The floor of the den chamber may be covered with beargrass, moss, and fir boughs. Animals move to den sites in late autumn regardless of the weather. However, final entry into dens is precipitated by a severe snowstorm (Servheen 1981). Apparently such a storm obliterates tracks leading to the den and seals the entrance. Animals typically spend up to 7 months dormant within the den. Depending on elevation and weather, entry may occur as early as October, with re-emergence in March or April. Grizzly bears do not hibernate, rather they enter a slight torpid state best described as winter dormancy. Considerable fat is deposited in autumn to provide for the energetic costs incurred during dormancy, and to provide insulation and body mass may increase 22%–40%. During dormancy, bears do not eat, drink, defecate, or urinate. Heart rate drops 5-fold from a non-dormant, resting rate of 40–50 bpm to a low of 8–10 bpm (Nelson et al. 1983b). Core body temperature decreases 4°C–5°C from an active range of 36.5°C–38.5°C. During dormancy animals are still cognizant of their surroundings and can awaken quickly. In association with dormancy grizzly bears recycle a nitrogenous waste product, urea, to synthesize protein such that animals emerging in the spring have a higher blood protein concentration than during the previous autumn (Nelson et al. 1983b). A better understanding of this process may help humans who need kidney dialysis.

Reproduction: Breeding in Montana may begin as early as late April and extend into late June or early July (Aune 1985). Follicular development in females begins while animals are still dormant (Hensel et al. 1969), as does testicular recrudescence in males. Although breeding is restricted to late spring–early summer, spermatogenesis may occur throughout the active period, with testicular regression in conjunction with preparations for winter dormancy. In Yellowstone National Park females may have 2 estrous periods during the breeding season. Males and females form pair bonds which may last 1–3 weeks (Murie 1981), although the breeding structure is polygamous.

Grizzly bears delay implantation. Following conception, embryos enter the uterus and remain dormant until late autumn when implantation occurs. Following a short period of post-implantation development (probably 2 months) parturition occurs. Young are helpless at birth and weigh 500 g. Mean litter size in Yellowstone was 2.24; whereas populations in Montana averaged 2.18 (Servheen 1987). Growth is rapid, although adult size is not reached until 4 (♀) to 6 (♂) years. Lactation extends for 1.5 to 2.5 years, but offspring typically stay with their mother for 2 to 3 years.

Females first successfully breed at 4.5–5 years and will produce litters at intervals of 2–3 years. Males also reach sexual maturity at 4.5 years of age.

Status: Listed as a threatened species in the continental United States in 1975. Since this time, significant efforts have been made to develop and institute recovery plans, particularly within Montana. Currently, Montana's population numbers about 500 individuals.

Pasitschniak-Arts, M. 1993. *Ursus arctos*. Mammalian Species 439:1–10.

ORDER ARTIODACTYLA—EVEN-TOED UNGULATES: PRONGHORN, BOVIDS, AND CERVIDS

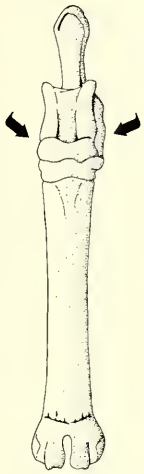


Fig. 74. Fusion of metacarpals and metatarsals into cannon bone, position of digits 3 and 4 and vestigial digits 2 and 5 (arrows).

The order Artiodactyla is comprised of a small but diverse group of 211 species organized within 81 genera among 9 families. This is 1 of 2 orders of hooved mammals, the other being the Perissodactyla (odd-toed ungulates) such as horses, tapirs, and rhinos. The name "Artiodactyl" is derived from the Greek arti meaning "even-numbered" and daktylos which means "toe." The more generic term ungulate refers to hooves, which are modified claws of keratin that cap the digits (phalanges). Artiodactyls are native to a wide region of the world with the exception of Australia, New Zealand, New Guinea, and the West Indies, and Antarctica.

This group is characterized by the unique structure of its foot; body weight is borne on the 3rd and 4th digits, with the 1st, 2nd, and 5th toes being absent or at best vestigial (Fig. 74). Tracks of deer and moose on soft ground may show impressions of the 2nd and 5th digits, the "dew claws." Fusion of the 3rd and 4th metatarsal and metacarpal bones into "cannon" bones streamlines the feet and provides rigid support for the animal's weight. Further modifications of the pectoral and pelvic girdles, the head of the humerus and femur, and the fusion of long bones (ulna to radius, fibula to tibia) significantly decrease limb rotation while strengthening and elongating its lever system. Artiodactyls have "unguligrade" foot posture, and walk on the tips of their digits.

Dentition is specialized for a herbivorous diet. All species native to Montana lack upper incisors and, with the exception of elk and caribou, lack upper canines (Fig. 75). Cheek teeth may be either brachyodont (low-crowned; as in deer, elk, moose, and caribou), or hypsodont (high-crowned; in pronghorns and bovids such as bison, mountain goats, and bighorn sheep), and selenodont (with crescent-shaped cusps). A grinding surface of alternating dentine and enamel continually provides a hardened expanse, even as the cusp wears down with age. Also, cusps on the molariform teeth are situated to allow the upper and lower jaws to rotate from side to side. This motion can be contrasted with the cutting action of jaws of felids and canids that allow food to be quickly sliced and swallowed. Most artiodactyls have a 4-chambered stomach which is specialized to digest cellulose. Anaerobic bacteria cultured within the largest chamber, the rumen, break down cellulose through the action of the secreted enzyme cellulase. Once the food is initially processed in this manner (the result being termed "cud") it is regurgitated into the mouth and remasticated. This "chewing of cud," a process termed rumination, is from which the term ruminant is derived. This

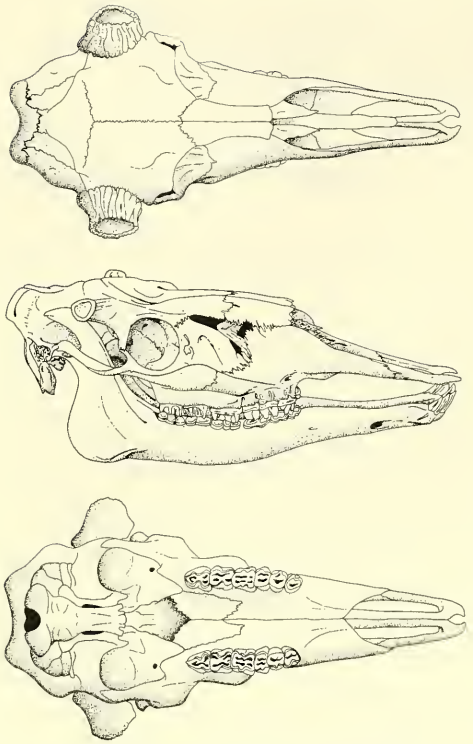


Fig. 75. Skull of an artiodactyl (*Alces*).

procedure may occur several times; each time a portion of the dissolved food (in the form of organic acids) is absorbed as nutrients through the rumen lining. Once this food has been sufficiently digested the food is then passed from the mouth a final time, moving into the remainder of the stomach (the reticulum, omasum, and abomasum) where water is absorbed and protein digestion occurs. This is an efficient process through which a high percentage of the nutrient quantity of most plant materials is extracted and ultimately absorbed. Such a digestive strategy allows these species to consume large amounts of plant material quickly and then process it in the relative safety of cover. Omnivores, such as the black bear and raccoon, may also eat large quantities of plant material but lack such a sophisticated plant-processing system, thus they are inefficient in this regard (as is shown by the undigested plant materials, berries and grasses, in their feces).

Although artiodactyls over the world range from the 0.7 kg mouse deer (*Tragulus*) of Asia to the 4,500 kg hippopotamus (*Hippopotamus amphibius*) of Africa, those in Montana are a bit more similar in size. The state's smallest ungulate is the pronghorn, at 50 kg and its largest, the bison, may weigh up to 900 kg.

Of 12 species native to North America north of Mexico, 8 occur in Montana (exceptions are the collared peccary, muskox, Dall sheep, and caribou). Most of the Montana natives, except the bison, are important game and attract tens of thousands of hunters each autumn. Countless other individuals visit Montana to simply enjoy and photograph these species.

All male and some female artiodactyls in Montana possess horns or antlers used for defense and social dominance. These appendages distinguish taxonomic groups; the antilocaprid and bovids have horns, while cervids possess antlers.

Horns develop from skin laid down internally over a bony core, off the frontal bone. With 1 exception (pronghorn), these epidermal sheaths grow throughout life. They are unbranched (except that of the pronghorn), although they may curve (e.g., bighorn sheep). Antlers are also extensions of the frontal bone but they are temporary and are shed each year. During their growth phase, they are covered by a thin layer of haired skin termed velvet. After the antlers are completely formed, the velvet sheath sloughs off leaving the polished, bone exposed. These bony structures are shed each year after the mating season. Antlers become more elaborate each year as the animal ages, exhibiting distinctive branching or palmated patterns.

Family Antilocapridae—Pronghorn*

Pronghorn
Antilocapra americana

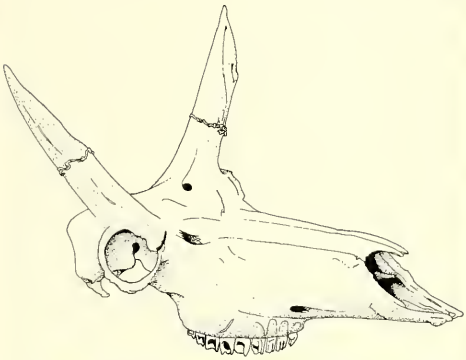


Fig. 76. Skull of the pronghorn (*Antilocapra*).

Pronghorn (*Antilocapra americana*). See plate 13.

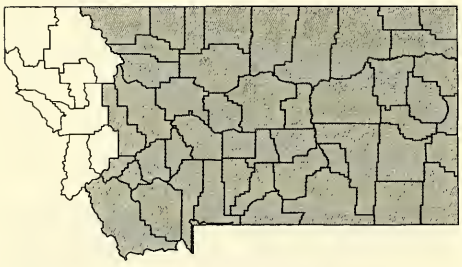
Scientific Name: The pronghorn was first described by George Ord, in 1815, from specimens collected by the Lewis and Clark expedition along the Missouri River, in central South Dakota. Ord was 1 of our 1st preeminent naturalists who, in 1812 with several other individuals, founded the Academy of Natural Sciences of Philadelphia. Originally identifying this species as *Antilope americanus,* Ord changed this 3 years later to its present name *Antilocapra americana.* The generic designation *Antilocapra* is from the Greek and Latin combination antholops which means "antelope," and capra which means "she-goat," respectively. The specific epithet *americana* is the Latinized form for "America," the origin of the type species.

Description: The pronghorn is small-bodied, compactly built with long, thin legs. Meriwether Lewis was the 1st to scientifically describe this species after killing a specimen on 14 September 1804. His description is accurate today:

> "... in my walk I Killed a Buck Goat of this Countrey, about the hight of the Grown Deer, its body Shorter, the Horns which is not very hard and forks 2/3 up one prong Short the other round & Sharp arched, and is imediately above its Eyes the Colour is a light gray with black behind its ears down its neck, and its Jaw white round its neck, its Sides and its rump round its tail which is Short & white verry actively made, has only a pair of hoofs to each foot. his brains on the back of his head, his Norstral large, his eyes like a Sheep—he is more like the Antilope or Gazella of Africa than any other Species of Goat." (Moulton 1987a:71)

In addition, a large patch of black hair occurs below the ears on males (subauricular region). Very large brown eyes are set in large, bony sockets; this latter characteristic can be used to readily identify this species' skull (Fig. 76; Foresman 2001). The coarse pelage consists of hollow hairs which greatly increase its insulating capacity. All males

* For representative skull characteristics of this taxonomic family refer to Fig. 76.



Map 101. Distribution of pronghorn, *Antilocapra americana.*

and many females have horns which are unique in 2 respects: they are forked, as indicated in Lewis' description above (in males only; from which the vernacular name, "pronged-horn" is derived), and deciduous, being shed each winter. Horns project from the supraorbital region, directly above the eye sockets; those of males are much larger than females. The pronghorn should not be confused with any other artiodactyl in Montana. Its small body form (0.5–0.66 times the size of white-tailed deer), unique color, large rump patches (with a small, non-descript tail), distinct horn shape, and strict grassland preference sets the pronghorn apart.

Measurements: [cm(*n*); Buck 1947]: TL = ♂ 133.8(36)/♀ 135.9(12); Ta = ♂ 13.5(36)/♀ 12.7(12); HF = ♂ 37.6(36)/♀ 36.6(12); E = ♂ 12.2(36)/♀ 15.0(12); M [kg(*n*); B. O'Gara, pers. comm.] = ♂ 59.0(30)/♀ 50.0(90). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The pronghorn is endemic to western North America, with a spotty distribution from southern Alberta and Saskatchewan, southward in a band through Montana and North Dakota, to central Mexico. This distribution extends in an east–west direction from eastern South Dakota and central Texas, to extreme northeastern California and Central Baja California.

Ecology and Behavior: Pronghorns prefer grassland and sagebrush habitats, although a few populations may live in the desert. A variety of plant species are eaten, but browse, in particular sagebrush, is most important during winter, making up over 80% of the diet. Forbs, such as fringed sage, may also be eaten at this time. Forbs such as eriogonum, wild blue flax, and penstemon predominate in the summer diet of Utah herds, supplemented by grasses as they green up. In central Montana, pronghorn may make use of cultivated fields of alfalfa heavily in autumn.

Pronghorn have distinct summer and winter ranges. Large aggregations of animals that were forced together due to snow conditions break into smaller groups, segregated by sex, and move in spring to summer ranges. Winter home-range size (6.5–22 km^2) in Montana varies with local topography as well as age and sex of animals. Summer range sizes are also influenced by topography but are generally smaller (0.2–4.34 km^2).

Herds are the focus of pronghorn social organization. A dominance hierarchy develops within female groups, which decreases competition for resources. Female herds use the territories of several adult males. Bachelor herds also form dominance hierarchies that determine which males (usually larger and older ones) acquire the territories essential for breeding.

Territorial behavior in males is seasonal, driven by an increase in testosterone. Older males become reproductively active before younger males. Males establish territories which they defend when females come into estrus. Established territories are often separated by no-man's lands, thus adults rarely confront one another. Bachelors may enter territories but resident males quickly confront and defeat them. Territories are marked by urine, feces, and secretions from subauricular glands.

The hormonal cycle that controls territorial behavior also controls horn growth and shedding of horn sheaths. Horn sheaths begin to grow in January reaching maturation by July, however, formation and hardening of underlying horn does not occur

until September. Shedding of horn sheaths occurs between late October and early December, 2 months after the rut. In each successive year the prong of the horn is enlarged and elongated.

Pronghorn have acute vision, olfaction, and hearing, useful for living in open habitats, where protective cover is not available. Their vision may be comparable to a human looking through 8× binoculars. Anyone who has approached these animals is well aware that pronghorn are quite sensitive to rapid movements, even at great distances, but seemingly ignore humans who are motionless, even close up. Thus pronghorns would recognize wolf packs on the move at a distance, but not a solitary predator waiting in ambush. However, pronghorn are able to run at speeds over 37 km/hour for short distances (Mitchell 1980) and may continue with speeds of 25 km/hour for longer distances. Such speeds would outdistance natural predators.

Olfaction has an important role in individual recognition and determination of reproductive status. Several glands produce oily, volatile secretions. Subauricular glands develop and become active in response to reproductive hormone levels. Glands in each rump patch, and a median gland lying in the middle of the back, about 25 cm in front of the tail, are associated with arrector pilli muscles and hair follicles and enhance airborne dispersion of secretions. When alarmed, hairs on the rump patch are raised providing a visual cue, that can be seen for a great distance, and a means of dispersing these chemosignals. Additional pheromones, secreted in urine, are used by both males and females to signal reproductive status. Female urine during estrus contains chemosignals which relay this condition to males. Males may place their own scent over a female urine to conceal information from other males (Moodie and Byers 1989).

Although common and often locally abundant today, pronghorn populations have undergone remarkable changes. As many as 35 million animals were present when Europeans came to North America; by 1924 <20,000 pronghorn were present of which about 3,000 occurred in Montana. Intensive management efforts rebuilt the population which now numbers nearly 1 million individuals.

Reproduction: Breeding in Montana extends from mid-September until early October. Testicular recrudescence occurs mid-to-late March, with maximal development by August. Spermatogenesis may continue throughout the year, although testicular regression occurs in December and extends through February, with little spermatogenic activity. The breeding system is polygamous. Gestation lasts about 252 days with parturition in late May to early June. Twins are the rule at birth although 4–7 ova are ovulated and fertilized. Blastocyst development in the bicornuate uterus results in tubular thread-like embryos. These embryonic threads become tangled and knotted, leaving the fetal membranes of many embryos damaged and unable to acquire the needed nutrients for continued development. Death by malnutrition occurs. If more than 2 embryos survive this early stage further embryonic loss occurs as the fetal membranes of 1 embryo literally spear those of an adjacent embryo. In this manner only 1 embryo in each uterine horn survives.

Pronghorn demonstrate the highest rate of maternal investment among ungulates (Byers and Moodie 1990). Offspring grow rapidly. Within 4 days they can outrun a human and then begin foraging on their own by 3 weeks of age. Yearling males may reach sexual maturity at 1 year of age but do not successfully breed until 2 years of age. Females are sexually mature in the autumn of their 2nd year at 16 months of age although mating has been documented at 5 months.

Status: Common and locally abundant. About 43,000 animals are harvested annually.

O'Gara, B. 1978. *Antilocapra americana.* Mammalian Species 90:1–7.

Family Bovidae—Bovids*

Bison
Bos bison

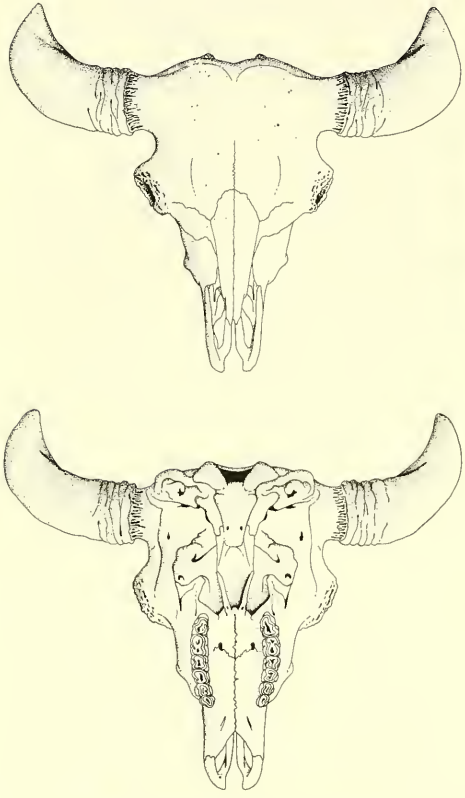


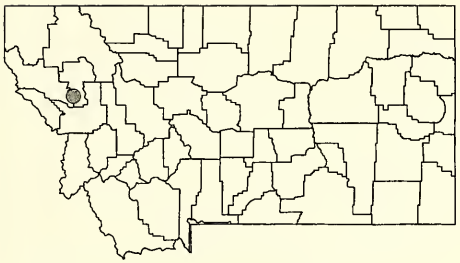
Fig. 77. Skull of a bovid (*Bos*).

Bison (*Bos bison*). See plate 13.

Scientific Name: The bison was first described by Carolus Linnaeus in 1758, from specimens obtained in what is now eastern New Mexico. Originally identified as *Bos bison,* the name was changed to *Bison bison* in 1888, and later was returned to its original form. Both the generic and specific epithets are derived from the Greek bisōn which means the "original wild ox."

Description: The bison is the largest North American artiodactyl; adult males weigh nearly 50% more than the largest of Alaskan moose with weights >1,000 kg recorded. The massive head (much larger in males than females) gives way to a large, muscular shoulder hump. From the shoulders, the body tapers markedly to the hindquarters which supports a short, tufted tail. Although the legs are short, bison are nearly 1.8 m tall at the shoulders. Both males and females have large but short black horns, that curve upward and inward and end in

* For representative skull characteristics of this taxonomic family refer to Fig. 77.



Map 102. Distribution of bison, *Bos bison*.

sharp tips. Long brown pelage which covers the animal from its head to behind its forequarters gives way abruptly to short, slicker hair on its hindquarters. In all respects, males are proportionately larger and more robust than females.

Measurements: [cm(n); Meagher 1986]: TL = ♂ 3040–3800/♀ 2130–3180; Ta = ♂ 330–910/♀ 300–510; HF = ♂ 580–680/♀ 500–530; ear = ♂/♀ none; M [kg(n); Meagher 1986] = ♂ 544–907/♀ 318–545. Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The bison was originally widely distributed across North America from Alaska across western Canada, extending southward across nearly all the continental United States and northern Mexico. Today the bison is isolated in parks, reserves, and private ranches. Free-ranging populations are primarily in Yellowstone National Park, Wood Buffalo National Park adjoining northern Alberta, the Northwest Territories, and the Mackenzie Bison Sanctuary in the Northwest Territories. The Montana distribution map indicates the location of the National Bison Refuge. Additional animals are held in many private herds.

Ecology and Behavior: Bison were nearly exterminated by the turn of the century due to excessive hunting. Original estimates placed the number of animals at 30 million as westward expansion brought Europeans into the northwest in the mid-1800s. As recorded by Meriwether Lewis 22 April 1805 near Williston, North Dakota:

> "... I ascended to the top of the cutt bluff this morning, from whence I had a most delightfull view of the country, the whole of which except the vally formed by the Missouri is void of timber or underbrush, exposing to the first glance of the spectator immence herds of Buffaloe, Elk, deer, & Antelopes feeding in one common and boundless pasture ..." (Moulton 1987b:60).

In 1886, bison were on the verge of extinction, and the Smithsonian Institution sponsored 2 expeditions to Montana to collect live specimens for the United States National Museum. Led by William T. Hornaday, 23 bison were collected (100 were desired) northwest of Miles City and shipped to Washington, D.C. where they were displayed and used to establish a founder herd at the National Zoo (Berger and Cunningham 1994; Hornaday 1889). A few specimens were killed on this expedition and are owned by the University of Montana's Philip L. Wright Zoological Museum and they are displayed at the Agriculture Museum in Fort Benton.

By 1903 only 1,644 animals remained; some in Yellowstone National Park and Wood Buffalo National Park, with a majority in private herds or zoos. Many efforts were made to establish new herds and rebuild existing ones. One of the earliest began with the formation of the National Bison Range, in western Montana, in 1908. A nucleus of 14 male and 26 female bison were introduced in 1910 (Berger and Cunningham 1994), and today a stable population of 350–400 animals is maintained. The sum of these efforts have produced a remarkable recovery with the number of animals now above 75,000.

Bison primarily occupied the central and northern grasslands of the continent from the tallgrass prairies, extending from Missouri to Minnesota, to the shortgrass prairies spanning Montana to Texas (Fig. 78). The Great Plains sport abundant sedges and

Fig. 78. Bison herd on the plains.

grasses which are eaten by bison, especially bluegrass, fescue, blue grama, and wheatgrass. Both bison and prairie dogs use the grasslands but in different, and synergistic, manners. Prairie dogs, by remaining stationary and selectively foraging on graminoids, produce islands of specialized vegetation distinct from the surrounding grasslands. Bison enhance this process; they also prefer graminoids and are drawn to these islands to feed and to wallow in the disturbed ground. The resultant plant communities have greater species diversity than those of the surrounding prairie, and these new ecosystems are used by many other species.

Bison are diurnal alternating between foraging bouts and passively ruminating. They can digest and retrieve nutrients from low quality native forage better than cattle, a situation which has renewed interest in commercial bison herds. Although direct competition would be suspected between plains ungulates such as bison and pronghorn, and between bison and range cattle, distinct habitat and food preferences restrict such interactions. On the National Bison Refuge in western Montana blue-bunch wheatgrass as well as Idaho and rough fescues accounted for nearly 88% of the annual diet.

Although most bison herds are limited in size and mobility because of captivity, free-ranging animals migrate seasonally. Movements from high elevation meadows to low elevation grasslands occur as food availability and snow levels change. Lewis and Clark observed such migrations in Montana, on 18 June 1805, while they portaged around the Great Falls of the Missouri, near present day Great Falls:

> "... Saw a gange of Buffalow Swiming the river above the falls, Several of which was drawn in to the rapids and with dificuelty mad Shore half drowned ... emence herds of those animals in every direction ..." (Moulton 1987b:307).

These movements have brought national attention to Montana and placed bison into the public and political arena. Since 1975, bison from Yellowstone National Park migrated northward onto adjacent private land in Montana during winter. The concern is not crop damage or competition with domestic cattle for forage, but rather the potential for exchange of brucellosis from bison to domestic cattle. Brucellosis is a bacterial disease that causes pregnant cattle to abort and males to become sterile. The federal government made a concerted effort over the past 60 years to eradicate this disease in cattle and certify states as being "brucellosis free." Nearly 50% of Yellowstone bison test positive for brucellosis, although this does not mean that the animals still carry the disease, nor are infectious. Furthermore, transmission of brucellosis from bison to cattle has not been documented in the wild. Regardless, the State of Montana and the livestock industry are so concerned about this potential that they have brought tremendous political pressure on the National Park Service to stop movement of bison out of the Park. Interim management plans adopted by the National Park Service, in response to this concern, have resulted in killing between 400 to well over 1,000 animals/winter.

Seasonal and yearly home range sizes are greatly influenced by habitat quality and food abundance. A free-ranging herd in southern Utah used an average of 52 km^2 in summer although this habitat was of low productivity. Unlike other Montana ungulates, bison form large, "mixed group" herds year-round comprised of animals of

most age and sex classes. Older females dominate these herds. In addition to mixed herds, mature males are solitary or form bull groups until the rut begins. In spring, cows with calves aggregate.

Bison on the open northern plains are often exposed to brutal winter conditions of extreme cold and deep snows. They have long, dense hair to insulate against these conditions; hair on their shoulders can exceed 15 cm in length, that on their forehead over 20 cm.

Reproduction: Although the breeding season may extend from late June through September, most successful copulations occur within a 2 week period between late July and early August. Females are polyestrous; wood bison, a subspecies found in northern Alberta, have a 3 week estrous cycle, and plains bison are probably similar. After a 277–293 day gestation, parturition occurs in April or May. With such synchrony in mating, most births are also synchronous. Births on the National Bison Refuge occur within a window of 14–21 days while those at Badlands National Park, South Dakota 19–23 days. Bison at Wind Cave National Park, South Dakota, may have a broader period of parturition (Green and Rothstein 1993). Single calves are the rule. Even by ungulate standards, bison calves are precocious. They can walk within minutes of birth and may attempt to graze within a few days. Weaning occurs between 8 and 12 months.

Both males and females reach sexual maturity between 2 and 4 years of age. Under normal circumstances when older males are present, males may not mate until 6 years of age with a majority of the calves sired by bulls 7–12 years of age.

Status: Common; maintained on private lands and federal refuges.

Meagher, M. 1986. *Bison bison*. Mammalian Species 266:1–8.

Mountain Goat
Oreamnos americanus

Mountain goat (*Oreamnos americanus*). See plate 14.

Scientific Name: The mountain goat was first described by H. M. D. de Blainville, in 1816, from specimens probably obtained from Mt. Adams, Washington. Originally designated *R[upicapra] americana*, the current name, *Oreamnos americanus*, was adopted in 1912. The generic designation *Oreamnos* is from the Greek combination -oreios, which means "of the mountain" and amnos meaning "a lamb." The specific epithet *americanus* is a Latinized referral to the country of origin of the type specimen.

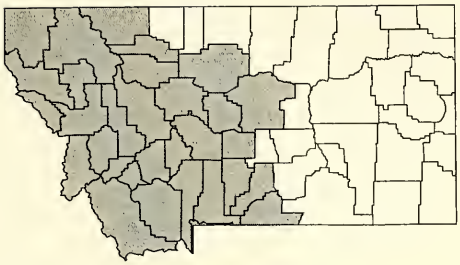
Description: The mountain goat is a small to medium-sized artiodactyl, compact and stocky in build. Both sexes have thin, tapering, black horns; those of males are slightly more robust than females. Pelage is distinctively white–yellowish, with long guard hairs and a dense wool underfur, accentuated by a beard which is more noticeable in males. The tail is small and nondescript, and feet are large with convex pads projecting from the hooves. The unique color of the mountain goat, its distinctive black horns, and its restricted habitat make identification easy. No other Montana species should be confused with the mountain goat.

Measurements: [cm(*n*); Smith 1993]: TL = ♂ 159.9(7)/♀ 157.1(36); Ta = ♂ 13.4(8)/♀ 10.2(36); HF = ♂ 36.2(8)/♀ 34.4(36); E = ♂ 13.3(5)/♀ 12.0(36); M [kg(*n*); Smith 1993] = ♂ 88.8(5)/♀ 71.5(29). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The mountain goat was originally distributed from southern Alaska through the Yukon and Northwest Territories and British Columbia and Alberta, reaching southern Oregon, western Montana, and southern Idaho. Since the 1930s, individuals have been introduced into additional mountain ranges in Oregon, Montana, Washington, South Dakota, and Colorado.

Since 1941, reintroduction efforts brought mountain goats to many isolated mountain ranges in western and central Montana where historically none lived (Mussehl and Howell 1971).

Ecology and Behavior: As the vernacular name implies, the mountain goat occupies mountainous terrain; preferably the highest, rockiest, and most rugged peaks where talus slopes and shear cliffs predominate. Diet varies seasonally, and by site, based upon availability. In Montana, shrubs (Buffalo berry and willow) are used extensively from summer to autumn, as are forbs such as St. John's-wort and beargrass, and sedges (Smith 1976; Thompson 1981). In



Map 103. Distribution of the mountain goat, *Oreamnos americanus.*

addition to beargrass, other forbs (milk vetch, tansy mustard, creeping hollygrape) and sedges become more important during autumn and winter at which time grasses (fescues, bluebunch wheatgrass, purple reedgrass) are prominently eaten. Buffalo berry and curl-leaf mahogany are also part of the winter diet in some Montana mountain ranges, as are conifers. Animals forage in early to mid-morning and toward evening along ledges and among rock outcrops, as conditions permit. Animals in the Swan Mountain Range (as well as other sites in Montana and Idaho) feed at all hours of the day, at intervals of 1.5–3 hours and may forage into the night. During snow-free months, animals forage in alpine meadows; as snows accumulate mountain goats retreat to talus slopes and steeper terrain where stepped ledges are blown free of snow.

Mountain goats require additional sodium in their diet during spring and summer and may travel several miles to use natural salt licks (Singer 1978) or to access salt licks established for livestock (Thompson 1981).

Seasonal migrations occur, particularly along an altitudinal gradient, with heavy snow bringing animals to lower elevations. Horizontal distances of 16 km or more may be covered. Annual home range sizes for adult males range from 6.3 km^2 in Glacier National Park to 22 km^2 in the Sawtooth Range southeast of the park (Thompson 1981) and 21.5 km^2 in the Sapphire Mountains of western Montana (Rideout 1977). Female home ranges are roughly comparable (8.9 km^2 in Glacier National Park to 24 km^2 in the Sapphire Mountains). Considerably smaller home ranges occur in the Bitterroot Mountains (Smith 1976).

During spring and summer, adult males are primarily solitary, although groups of 2–3 occur. Average group size in the Bitterroot Mountains is 1.5 animals (Smith 1976). Adult females form larger, mixed groups including their offspring and non-related subadults, although even here group sizes remain small. One exception occurs where food is limited or a desired salt lick concentrates individuals. In Glacier National Park, groups of over 40 individuals congregated at a natural salt lick at the base of Running Rabbit Mountain and provided the park with a strong tourist attraction.

One unique aspect of mountain goat behavior is that adult males are subordinate to not only adult females but even to juveniles. This situation may result, in part, from limited food resources; where limitations do not occur, males are dominant. As rut approaches in the autumn, males mark vegetation with scent from glands at the rear base of their horns. They also mark territory with urine.

Both mountain goats and bighorn sheep can be aged by annual growth rings which form on their horns; however those of goats are more subtle. With renewed growth in the spring of the animal's 2nd year (22 months of age) the 1st ring is formed, and each subsequent spring another ring is added.

Although smaller in body size than bighorn sheep, the feet of mountain goats are larger and more specialized for rock and snow travel. The hooves provide a larger surface area to support the animal's weight on crusted snow and the spongy, protruding pads provide significant traction to navigate smooth rock surfaces. Their dense, thick underfur is an obvious adaptation for severe winter conditions. However, their lower critical body temperature (the temperature at which they must expend energy to maintain their homeothermic condition) is only $-20°C$, far higher than true Arctic animals, indicating that their pelage is not

as effective in this regard. Both smell and vision are acute and mountain goats behave in a manner similar to the pronghorn. If an animal (human) is moving it is readily detected even from a distance of 800 m. However, if the object remains stationary it is not uncommon for mountain goats to blunder onto them.

Reproduction: Breeding in Montana begins in late October with greatest activity occurring during November and December. Estrus may last 2–3 days. Gestation length has been variously recorded as 147 days, or 178–182 days; the latter range is probably more accurate. Parturition occurs in late May or early June; single offspring are produced although twinning does occur, and triplets have been documented.

Kids are precocial at birth, able to jump and hop, although in an uncoordinated fashion, within hours of birth. By day 4 kids can scrabble across rough, steep terrain. Both males and females reach sexual maturity at 2 years of age.

Status: Common; animals have been introduced into many isolated ranges formerly unoccupied. This species is legally hunted in Montana with >200 animals harvested in 1995.

Rideout, C. B., and R. S. Hoffmann. 1975. *Oreamnos americanus.* Mammalian Species 63:1–6.

Bighorn Sheep
Ovis canadensis

Bighorn sheep (*Ovis canadensis*). See plate 14.

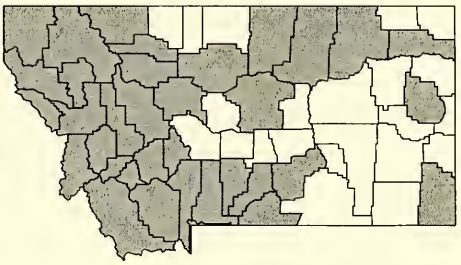
Scientific Name: The bighorn sheep was first described by G. Shaw, in 1804, from a specimen collected near Exshaw, Alberta in 1800, by D. McGillivray. The designation applied at this time, *Ovis canadensis,* is still accepted today. The generic name, *Ovis,* is derived from the Latin ovis meaning "sheep." The specific epithet, *canadensis,* is a Latinized reference to the country of collection.

Description: The bighorn sheep is a robust bodied, short-legged artiodactyl, brown to chocolate-brown in color, with sharply demarcated white on the muzzle, belly, hind legs, and rump. Tail is small and dark brown–black. Both sexes have horns, those of the male are massive and spiral forward toward the face.

Measurements: [cm(*n*); ♀ Hall 1981]: TL = ♂ 176.0(10)/♀ 116.6–188.7; Ta = ♂ 12.1(10)/♀ 7.7–13; HF = ♂ 46.0(10)/♀ 27.6–42.0; E = ♂ 13.9(10)/♀ none; M [kg(*n*)] = ♂ 112.6(10)/♀ 75.0(10). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The bighorn sheep ranges from southern British Columbia and

Fig. 79. Bighorn sheep ewe with young.



Map 104. Distribution of bighorn sheep, *Ovis canadensis.*

Alberta through the mountainous regions of the western United States into northern Mexico. This distribution is spotty and includes desert ranges of the southwest. Many populations in Montana are the result of reintroduction efforts since the 1940s (Mussehl and Howell 1971).

Ecology and Behavior: Bighorn sheep occur in a diverse variety of habitats throughout Montana, from the alpine meadows of Glacier National Park, to the lower Missouri and Yellowstone breaks. Rough, rocky terrain with steep cliffs in association with meadows or grasslands are required components of its habitat. Although not as agile a climber as the mountain goat, bighorn sheep are often sympatric with this species. However, bighorn sheep can eat a much broader range of foods and can live in much more arid habitats. In Montana bighorn sheep prefer grasses, such as bluebunch wheatgrass, Idaho fescue, and prairie junegrass (Klaver 1978; Tilton 1977). Forbs (pussy-toes, yarrow) and shrubs, notably green-bush, mountain mahogany, mountain maple, serviceberry, and sage, are important in winter. As with mountain goats, bighorn sheep make heavy use of natural or artificial salt licks, particularly by ewes in June and July following lambing (Butts 1980; Tilton 1977). Foraging is diurnal and feeding is interrupted by rest and rumination.

Seasonal home ranges are dictated by snow and food. Movements of up to 32 km between summer and winter ranges occur for Montana populations although, if conditions permit, animals will live in the same area year-round (Erickson 1972, Klaver 1978). Mean winter and summer home range sizes vary from 60–130 ha to over 202 ha respectively for both sexes (Butts 1980; Tilton 1977).

Bighorn sheep are social. Both ram and maternal groups (adult ewes and young) form. Subadult males remain with a maternal group until they reach 3 years of age and become dominant to adult ewes. The polygynous breeding system led to strong agonistic behavior between rams both prior to and during the rut. Dominance is established by behavioral displays and headlong clashes, for which this species is well-known. On the National Bison Range rams have a highly linear social hierarchy based on age; the older the individual the more dominant it is (Hass and Jenni 1991). Ewes, in contrast, form a stable, non-linear hierarchy that is age-related but requires fighting for high social status (Hass 1991). Elaborate behavioral strategies allow males access to females, who enter estrus at different times, during the autumn rut. Dominant males may "tend" ewes while they are

in estrus, less dominant individuals may attempt to draw a tending male away from the dominant male's ewe to provide just enough time to mate with her, a strategy termed "coursing." Subdominant males may simply try to keep ewes away from the main group until they can be bred, a behavior termed "blocking" (Hogg 1984).

Bighorn sheep populations have declined precipitously over the past century due not only to competition with domestic sheep for food but also to the transmission of diseases from domestic stock to native populations. Bighorn sheep are particularly susceptible to lungworm infections which produce a pneumonia-like condition. They also readily pick up mites from domestic sheep which can cause severe scabies and death.

Reproduction: Bighorn sheep mate in autumn; the rut in Montana and neighboring Idaho typically occurs mid-November to late December. Females are seasonally polyestrous; each estrous cycle lasts 2–3 days. Gestation lasts 174 days, thus lambing occurs in the spring, from mid-May to late June. Single offspring are the rule (Fig. 79). Although growth is rapid, sexual maturity does not occur in females until 2.5 half years of age. Males, because of the dominance status that is required for successful access to females, often do not mate until 7–8 years.

Status: Common; animals have been introduced into many isolated ranges formerly unoccupied.

Shackleton, D. M. 1985. *Ovis canadensis.* Mammalian Species 230:1–9.

Family Cervidae—Cervids*

Moose
Alces alces

Moose (*Alces alces*). See plate 15.

Scientific Name: The moose was first described by Linnaeus, in 1758, from specimens obtained in Sweden. The original nomenclature, *Cervus alces,* was changed to *Cervus americanus* for the 1st specimen described in the United States. This specimen was recorded in the western Adirondack region of New York by Clinton, in 1822. The present day designation *Alces alces* was 1st applied by Lydekker, in 1915.

The generic and specific designations, *Alces alces,* are from the Greek alkē which means "elk," the common name applied to the European form. All European and west Siberian populations of elk, although quite distinctive from east Siberian elk and North American moose, are now recognized as subspecies of *Alces alces,* along with the North American races (Groves and Grubb 1987).

Description: The moose is the largest of North American cervids weighing in ex-

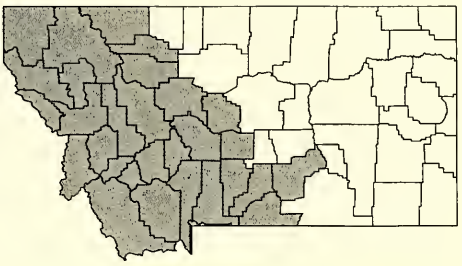
* For representative skull characteristics of this taxonomic family refer to Fig. 75.

cess of 595 kg in the northernmost regions of its distribution (Alaska). Morphologically, it is quite distinct from other members of the deer family. Color is black to dark brown, with lighter shading on its underparts and lower legs. Its body form is unusual and appears almost as a patchwork of varied pieces, "... put together by a committee." The massive body is supported on very long legs, from which the shoulders rise considerably above the rump. Its expanded, bulbous muzzle hangs over its mouth, and a long expansion of skin (the dewlap) hangs from its throat. Ears are large and expressive, while the tail is short and non-descript. Males sport large, palmate antlers.

Measurements: [cm(*n*); Smith 1993]: TL = ♂ 254.9(10)/♀ 249.1(10); Ta = ♂/♀ none; HF = ♂ 80.4(10)/♀ 80.2(10); E = ♂/♀ none; M [kg(*n*); Smith 1993] = ♂ 384.2(10)/♀ 377.5(10). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The moose occurs in the boreal parts of Eurasia and North America. It entered North America in the Pleistocene by crossing the Beringia land bridge which connected Eastern Asia and Alaska and has expanded its range across the Canadian provinces into Nova Scotia, and Maine. Its current distribution includes extensions in to Minnesota and the western United States. In the west, it is found along a narrow band spanning northeastern Washington and northern Idaho, extending along the Rocky Mountain chain through western Montana, northeastern Wyoming, and southeastern Idaho, into northeastern Utah.

Ecology and Behavior: Moose originated in the boreal forests of the north. They are closely tied to densely forested habitats but are a "disturbance species." In other words, they depend heavily upon woody vegetation, preferably in early successional stages, for forage; their food, such as willows and quaking aspen, appears quickly after fire or logging disturbances. Moose also prefer riparian regions and may spend early morning and evening hours feeding on emergent aquatic vegetation in shallow ponds, and submergent vegetation in deeper bodies of water. They can submerge completely while feeding on bottom pond vegetation. Their reliance on aquatic vegetation is correlated with the need for minerals, such as sodium, which are deficient in terrestrial browse (Belovsky and Jordan 1981).



Map 105. Distribution of the moose, *Alces alces*.

Preferred foods vary with season. In southwestern Montana's Gravelly Mountains (Knowlton 1960) forbs make up over 70% of the summer diet, primarily sticky geranium. Browse, predominantly willow, makes up the remainder of the diet. In the Gallatin Mountains of southcentral Montana, the diet shifts in autumn and winter, when browse accounts for 88 to essentially 100% of food intake with willows, alpine fir, silverberry, and serviceberry predominating (Knowlton 1960; Stevens 1970). During spring, browse is still preferred although a shift toward forbs begins.

In western Montana, particularly in the Yaak River region, dramatic population increases occurred since the early 1900s in response to large scale forest fires (Costain 1989). This trend has continued to the present as expanded logging activities provided the preferred early successional stages of forest growth. Multi-storied timber stands are important to moose as well, providing summer refugia from heat, and wintering areas when snow levels increase (Matchett 1985). A distinct shift in habitat during mid-winter occurs throughout Montana as animals move from open "browse" habitats

to more densely timbered patches (Costain 1989; Stevens 1970).

Developing in northernmost regions, the moose has evolved an anatomy which is ideal for the deep snows and extreme cold temperatures which it must confront for well over half of each year. Its heavy winter pelage may reach 254 mm in length, and provides significant insulation. Long legs and huge feet, the toes of which can splay out for added support, allow the moose to push through deep snows. Moose can wade with apparent ease through 2 m of snow, so deep that their belly drags the surface. They may, for short periods, contend with deep snows. However, when heavy snowfalls occur, they retreat to more densely canopied forests, where snow accumulations are less. Ambient temperatures as low as −30°C are accommodated without an increase in metabolic rate (Renecker and Hudson 1986). However, this specialization for cold environments may limit its southerly distribution since moose overheat easily. Upper thermal limits in the summer are between 14°C and 20°C; above these temperatures moose have to expend energy, by panting, to remain cool.

Moose are solitary and not territorial, although a cow will defend her calf. They maintain a relatively small home range from 1 year to the next and migrate seasonally, as do elk and deer. Winter home ranges are 4.8 km^2 for populations in northwestern Montana with summer and autumn values of 12.8–26.5 km^2 (Costain 1989; Matchett 1985). On a yearly basis, movement may occur over roughly 44.8 km^2. Although home ranges greatly increase during summer and autumn, most activity is concentrated in several local ranges among which the animal frequently moves.

Population densities in Montana vary greatly depending upon local habitat conditions. The northwest may have from 0.49–1.76 animals/km^2 (Costain 1989; Matchett 1985) whereas the southwest may support 3–10 animals/km^2 (Stevens 1970). During the rut both males and females are extremely aggressive. Male–male fighting may occur over a female and the huge antlers will be used for defense. Such battles can lead to death, although this is uncommon.

Both males and females use pheromones from scent glands and urine to communicate reproductive status. Pheromones in the urine of males can induce ovulation in females, as occurs in some rodents (Miquelle 1991).

One of the moose's most striking attributes is the remarkable development of the male's antlers. These body ornaments are palmated, unlike those of deer and elk, and become very large. Distance between the tips may reach 122 cm in Alaskan moose and a set of antlers can weigh nearly 41 kg (Caras 1967).

Wolves and grizzly bears are the only species, besides humans, which can prey upon moose. Young, or weak, individuals are most susceptible to attack. Heavy snow may hamper the ability of moose to avoid attack, especially if the snow cap can support the wolves but not the moose.

Reproduction: Testicular recrudescence and spermatogenesis begin in late summer in preparation for mating in early autumn. In Montana the rut begins early-to-mid September and may extend to late October. Moose are seasonally polyestrous. Estrous cycles are 20–28 days long within which a 24-hour period of receptivity (estrus) occurs.

After a gestation of 234–246 days 1 offspring is born, although twinning is not unusual and triplets can occur. Litter size and age at breeding are strongly influenced by nutrition. Development is rapid with calves growing over 1 kg/day. Both sexes may become reproductively active as yearlings (at 16–18 months of age). Most yearling males, although, are not successful in competing with older bulls for cows.

Status: Common; classified as a game species. Over the past 10 years about 600 animals have been taken annually.

Franzmann, A. W. 1981. *Alces alces*. Mammalian Species 154:1–7.

Elk
Cervus elaphus

Elk (*Cervus elaphus*). See plate 15.

Scientific Name: First described by Carolus Linnaeus (1758), in 1758, from European specimens. The name *Cervus elaphus* was applied to animals locally known as red deer. In North America, Erxleben (Hall 1981:1085) described a similar species from Quebec, Canada, naming it *Cervus canadensis,* to which the common name "elk" was applied. Unfortunately, this led to confusion which lasts to this day as the word elk was already used for the European moose. Further, the European red deer and the North American elk are the same so, by convention, the proper taxonomic appellation today is *Cervus elaphus.* The generic designation *Cervus* is from the Latin cervus which means "deer;" the specific epithet *elaphus* is from the Greek elaphos which also means "deer" or "stag."

Often the term "wapiti" is applied to the American elk, although it more appropriately designates a larger group of animals within the genus *Cervus* (Murie 1951). When the European red deer was considered distinct from Asian and North American forms, the term wapiti was used when identifying non-European populations.

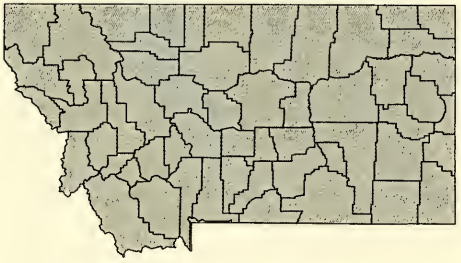
Description: The elk is a large cervid 2nd only in size to the moose. General body color is brown to grayish-brown with much darker, often nearly black legs and neck. Head is dark brown, while venter and rump are a lighter tawny color. A distinct, dark brown mane highlights the throat and the tail is short and non-descript.

Measurements: [cm(*n*); Quimby and Johnson 1951]: TL = ♂/♀ 242.3(12); Ta = ♂/♀ 14.2(12); HF = ♂/♀ 66.9(12); E = ♂/♀ 21.2(12); M [kg(*n*); Quimby and Johnson 1951] = ♂/♀ 331(10). Dental formula: i 0/3, c 1/1, p 3/3, m 3/3, total 34.

Distribution: Historically, elk inhabited a wide portion of the continental United States extending northward throughout Alberta, eastern British Columbia, Saskatchewan, and southern Manitoba. The southern boundary extended from northern New Mexico to portions of Georgia and South Carolina. Except for transplantation to the eastern portion of the country, the elk is now confined primarily to the western region of the continent. Numerous states including Montana, and private groups such as the Rocky Mountain Elk Foundation, have reestablished herds throughout the west for hunting.

Ecology and Behavior: In the Rocky Mountain region, elk migrate from winter to summer ranges as weather and food dictate and use diverse habitats dependent upon local availability. The Sun River drainage lies in westcentral Montana near the town of Augusta; eastern portions of the Continental Divide and the Bob Marshall Wilderness are used by this elk herd.

In late June, animals move to their summer range leaving the grasslands and passing through transitional, low-elevation forested stands of limber pine and quaking aspen, before reaching higher elevation for-



Map 106. Distribution of the elk, *Cervus elaphus*.

ests dominated by Douglas fir, lodgepole pine, Engelmann spruce, and subalpine fir (Edge et al. 1987; Knight 1970). Here, dispersed among more open parks, elk spend summer and early autumn. They feed predominantly on forbs (asters, daisies, dandelions, and elk thistle) and grasses (alpine bluegrass, brome grass, and wheatgrass in July; timothy and bluegrass by October). In autumn elk move into more timbered stands before migrating downslope to valley grasslands, where they concentrate in large numbers, for winter. The winter range is dominated by a bluebunch wheatgrass, Idaho fescue, and rough fescue. Spring provides new growth on the winter range, but by April animals are on the move again toward their summer range. Elk use the same winter and summer ranges from year to year. Calves, following their mothers, learn the same areas and migration routes to and from these areas.

Until the 1960s, elk were thought to benefit from logging activity as removal of timber creates abundant forage. However, it has been realized that loss of cover and increased disturbance (and hunting pressure) due to increased roading have a significant negative impact (Lyon 1971).

Every year male elk grow and subsequently shed antlers. Growth is initiated in April or May (to some degree influenced by the age of the animal) from germinal tissue (pedicels) on the frontal bones which lie on top and to the side of the skull. Bulls 1 year old begin this life-long cycle, with each year bringing larger, often more elaborate efforts. First year's growth results in spikes of bony tissue which harden in September. The overlying skin tissue, the "velvet," which provided nutrients to the developing antler, loses its blood supply, withers, and sloughs off. The antler at this stage is mature (although technically dead) and ready to impress females (cows) and other bulls. Antlers provide a means for defining a rigid social hierarchy and allowing cows to assess a male's dominance. They also provide legitimate armament for males to secure and maintain a harem of females. Mature bulls have formidable antlers. The main beams may exceed 152 cm in length with a base circumference of 15–20 cm. What is so remarkable is that this growth of bone (sometimes in excess of 4.5 kg/antler—Wolfe 1982) occurs so rapidly, within 4–4.5 months with growth rates of 2 cm/day (Goss 1970). Antlers are held throughout the autumn rut and into winter. They break off in late February when hormonal changes weaken the attachment between the antler proper and the pedicel from which it grew. Unfortunately the size and degree of branching do not indicate age but instead reflect the nutritional status and genetics of the male.

Predation on elk by mountain lions occurs predominantly during winter when elk are concentrated and often hampered by deep snows. In Idaho usually older and weaker elk are captured, or the very young (Hornocker 1970; Seidensticker et al. 1973). Because 1 elk every 3 weeks will sustain an adult lion, lions do not significantly affect elk populations.

Reproduction: Elk mate in autumn and have a polygynous breeding system. Dominant males maintain a harem of 5–6 cows (Knight 1970); larger harems (5–15) are maintained by Rocky Mountain elk in Wyoming (Altman 1960). Changes in day length initiate testicular recrudescence in September and lead to the "rut" (Sadlier 1987). Bulls become more aggressive and begin to bugle, providing one of the most unique sounds in the forest. This high pitched sound was translated by Olas Murie

(1951) as: A-a-a-a-ai-e-eeeeeeee-eough! e-uh! e-uh! Once heard, it will never be forgotten. Bugling attracts females as it warns the males away. Serious battles ensue if another male tries to entice a cow from the harem. Antlers provide the weapons for battle and can inflict fatal wounds.

Estrus occurs in late September to early October and gestation is 246–250 days, with parturition in early June (Morrison 1960; Morrison et al. 1959). A developmental growth curve constructed from elk trapped in Yellowstone National Park and maintained on the National Bison Range (Moiese) can be used to age calf fetuses and determine conception dates in managed herds. If conception does not occur during 1 estrus (these only last for 17 hours) females will recycle in slightly over 21 days. Estrus may recur 3–4 times before females enter a non-reproductive state (anestrus) until the following autumn. Conceptions in January will produce calves in September. These calves have little time to build up sufficient reserves to survive the winter. Such out-of-season births in the free-ranging population overwintering on the National Elk Refuge, in Jackson, Wyoming, indicates that this phenomenon may be more common than previously thought (Smith 1991). These findings are significant because both females and males during the hunting season may miss the 17-hour window of opportunity for mating. If this occurs, conception is delayed for at least 3 weeks. Most management strategies now set primary hunting seasons after 1st estrus periods and thus reduce the number of late season births.

Males reach sexual maturity at 2 years of age although they rarely mate until they are 4–5. Females reach sexual maturity during their 3rd season, at 28 months. Most commonly, single calves are born although twinning does occur. Calves have a spotted coat which provides a degree of protection. This is most useful during their 1st days of life while calves hide in tall grass as their mother feeds. Within 6 days, this behavior gives way to a more curious attitude and young are more likely to stay with their mother and run when threatened. At this time they are most vulnerable to predation by coyotes, wolves, and mountain lions.

Status: Common; classified as a game animal. The elk is Montana's most important game species attracting thousands of hunters from out-of-state along with tens of thousands of Montanans. In 1995, 138,102 hunting licenses were purchased and nearly 23,000 elk were harvested.

Mule Deer
Odocoileus hemionus

Mule deer (*Odocoileus hemionus*). See plate 16.

Scientific Name: The mule deer was first described by Rafinesque, in 1817, from a specimen collected in South Dakota. The accepted designation for the genus today is *Odocoileus* and is from the Greek combination odous which means "tooth," and koilos which means "hollow," thus "hollow tooth." This description refers to the hollow-appearing cusp pattern of the molariform teeth. The specific epithet *hemionus* is from the Greek hēmionos which means "mule," reference to the large, mule-like ears.

Description: The mule deer is a medium-sized artiodactyl, gray to dark brown in color with a white–yellow rump patch, a white throat patch, and a black, "horseshoe-shaped" marking on its forehead (the latter is much more prominent in males). Ears are large and rounded. The tail is narrow, with a white base and underside and black tip. Tail color varies in Montana populations. Tarsal and metatarsal glands are prominent and elongated. Males have antlers whose main beam branches, and then branches again, producing a dichotomous "tree" (Fig. 80). The mule deer, on 1st glance, could be easily confused with the white-tailed deer. Its larger body frame, darker color, black-tipped tail, longer, more pronounced metatarsal glands, and branching antlers (in males) allow its identification. Two behaviors readily distinguish the species, particularly when animals are too distant for other characteristics to be seen. When excited, mule deer bound on all fours almost as although they were jumping on pogo sticks, a behavior termed "stotting." White-tailed deer do not stot, but when excited will "flag" their large, white tail back and forth.

Measurements: [cm(*n*); tail and ear measurements Smith 1993]: TL = ♂ 168.7(10)/♀ 155.0(10); Ta = ♂ 19.2(90)/♀ 17.1(32); HF = ♂ 51.0(10)/♀ 48.7(10); E = ♂ 21.1(38)/♀ 19.7(6); M [kg(*n*)] = ♂ 92.2(10)/♀ 72.3(10). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The mule deer is endemic to North America, and widely distributed across western North America from the Yukon and southern Northwest Territories, through British Columbia, Alberta, Saskatchewan, and western Manitoba. Within the continental United States, it extends from the Pacific coast to Minnesota and Iowa, and southward into central Mexico.

Ecology and Behavior: Mule deer prefer open montane habitats and sagebrush slopes. They live in the sub-alpine coniferous forests of western Montana and the

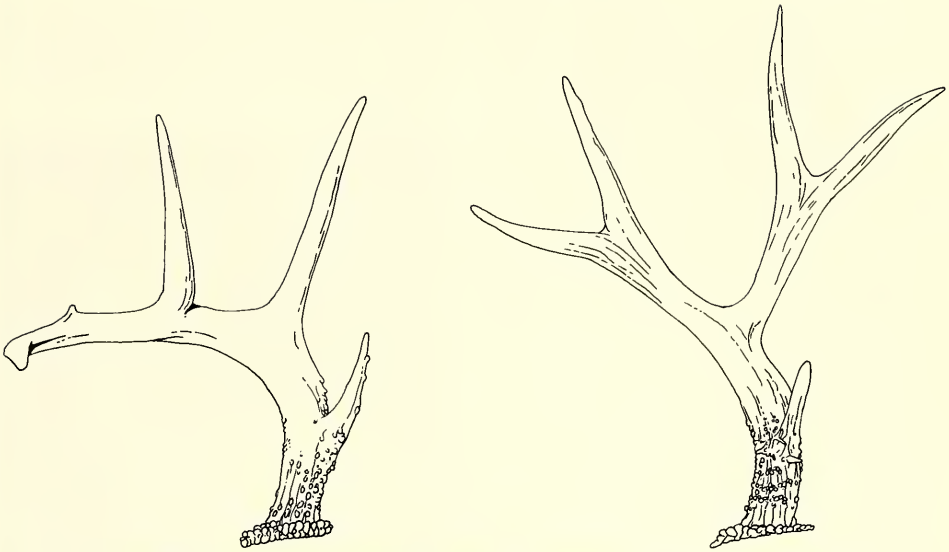
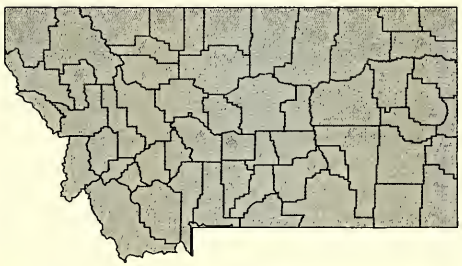


Fig. 80. Comparison of antlers in male a) white-tailed deer, and b) mule deer.



Map 107. Distribution of the mule deer, *Odocoileus hemionus.*

hardwood forests of the southeast. Mule deer may be sympatric with the white-tailed deer; where this occurs mule deer prefer higher elevation, more open sites.

Although mule deer are commonly thought to be entirely "browsers," they are actually intermediate feeders and eat about equal proportions of woody browse and herbaceous forbs. In the Missouri River breaks of central Montana forbs, in particular yellow sweetclover, account for nearly 45% of the total intake and browse accounts for the other 55%, with skunkbrush sumac, snowberry, and rose predominant. In autumn, mule deer eat fewer forbs and more browse. By winter, browse, particularly big sagebrush and Rocky Mountain juniper, predominates. In spring, browse is still the most important food source, although grasses, particularly Sandberg bluegrass, are eaten as they green up. In the coniferous forests of western Montana mule deer eat ponderosa pine, Douglas fir, snowbrush, chokecherry, and huckleberry supplemented by balsamroot and bull thistle as additional important forbs (Knoche 1968). This is by no means an exhaustive listing of plants mule deer eat. In general, browse use predominates throughout the year, accounting for 50 to >60% of total intake, with forbs accounting for 30%; and grasses making up the difference.

Mule deer are ruminants with a highly specialized, 4-chambered stomach. However, because they have a comparatively small stomach for a ruminant, food remains in the rumen for less than a day. This limits the degree to which fiber can be digested and thus the nutrient recovery that can occur from forage with high cellulose content. It also means, however, that the animal weighs less and can escape predators more easily.

Mule deer in Montana use an area of

from 40 to >1,000 ha depending on the abundance and quality of food and cover (Kraft 1989; Wood 1986). During the day, animals seek out rougher habitat which provides more protection from human disturbance and native predators. In such areas of eastern Montana higher population densities occur. Along the Missouri River breaks of central Montana, where agricultural lands are interspersed with rugged, non-timbered coulees, mule deer use cultivated lands from September to April. Animals routinely move into fields as darkness approaches and spend the night foraging before returning to the safety of the breaks at dawn. Barley fields are particularly preferred.

Seasonal home ranges occur in some portions of Montana, although in the Missouri River breaks year-round residency is the norm. Where migrations occur, movement to higher elevation summer ranges begins in spring as snows melt and births approach. In autumn, snows reduce food availability and bring animals down to lower elevations.

Both vision (binocular and color) and hearing are excellent, although stationary objects, as most hunters are aware, are often not recognized. Antler development begins in males in spring with loss of velvet and maturation of the bony component by September. Antlers are carried through autumn and winter and are shed in late winter to early spring. Specialized sweat glands (sudoriferous glands) are on the forehead in the horseshoe-shaped region of black hair seen in males. The activity of these glands increases as rut approaches; bucks rub these glands against vegetation marking it with pheromones to communicate social and reproductive status.

Reproduction: Breeding in Montana is seasonal. Rutting begins as early as mid-September, although the peak does not occur until mid-November/early December. Testicular recrudescence begins in August, peaking in early November. Females may mate during their 1st estrus but, more commonly, conception does not result until the 2nd or subsequent ovulations. Recurrent estrous cycles last 23–29 days, with a 24 to 36-hour estrus period ensuing. Up to 5 estrous cycles may occur during the autumn breeding period defining polyestry in this species. Gestation is 200–208 days with young born in June. Twinning is common, although the number of births/female is highly influenced by local food quality and availability. Young are weaned between 5–16 weeks of age.

Females do not reach sexual maturity until the 2nd year (at about 1.5 years of age). Males can breed as yearlings although most often adult female behavior and/or the presence of older, more dominant males precludes this possibility.

Status: Common; 1 of the most important game species in the state. In 1995, 200,618 deer licenses were sold and over 75,000 animals were harvested.

Anderson, A. E., and O. C. Wallmo. 1984. *Odocoileus hemionus.* Mammalian Species 219:1–9.

White-tailed Deer
Odocoileus virginianus

White-tailed deer (*Odocoileus virginianus*). See plate 16.

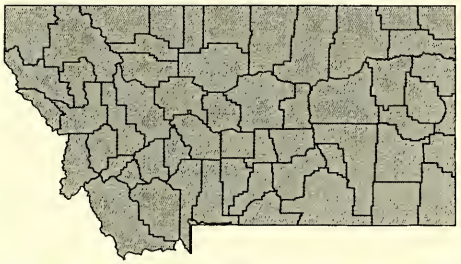
Scientific Name: White-tailed deer were first described by Zimmermann, in 1780, from specimens obtained in present day Virginia. Originally designated *Dama virginiana*, the present name, *Odocoileus virginianus*, was first recorded by Allen, in 1901. The generic distinction, *Odocoileus*, is from the Greek combination odous which means "tooth," and koilos which means "hollow," thus "hollow tooth" and refers to the hollow-appearing cusp pattern of molariform teeth. The specific epithet *virginianus* is Latin for Virginia, the origin of the type specimen.

Description: The white-tailed deer is a medium-sized artiodactyl with a predominant coat of brown broken by a white throat patch, white venter, and white underside of the tail. The vernacular name is derived from this latter characteristic; the tail is large and is "flagged" when the animal is threatened making the white underside highly visible. Ears are large although only two-thirds the size of those of the mule deer. Other distinguishing characteristics are the reduced, although prominent, metatarsal glands and, in males, antler shape where secondary tines arise from a single main beam (Fig. 80). Although white-tailed deer may be confused with mule deer at 1st glance, several distinct morphological and behavioral differences clearly distinguish the 2. White-tailed deer are slightly smaller in size and lighter in color. Differences in metatarsal glands, tail morphology, and color also identify these species, as does antler morphology in males. Finally, when agitated, white-tailed deer will gallop away prominently waving their white tails, while mule deer will most often demonstrate a bouncing gait (stott) without wagging their tails. Skull characteristics are also distinctive (Foresman 2001).

Measurements: [cm(*n*); Smith 1993]: TL = ♂ 186.9(442)/♀ 169.8(457); Ta = ♂ 28.7(449), MT 30.5(1)/♀ 25.1(462); HF = ♂ 49.8(444), MT 48.9(1)/♀ 46.7(464), MT 47.8(4); E = ♂ 16.0(168)/♀ 15.1(209); M [kg(*n*)] = ♂ 89.0(6)/♀ 61.6(7). Dental formula: i 0/3, c 0/1, p 3/3, m 3/3, total 32.

Distribution: The white-tailed deer is widely distributed throughout North America from the southern portions of the Canadian provinces to northern South America. Within the continental United States, it is not present in Utah and is rare in California and Nevada.

The white-tailed deer is a relatively recent immigrant into the northwest from a historical standpoint. Lewis and Clark recorded its presence during their expedition of 1804–1806, however it was not abundant. Populations actually declined with increased



Map 108. Distribution of the white-tailed deer, *Odocoileus virginianus.*

hunting pressure, but have been on the increase since the early 1940s.

Ecology and Behavior: As should be apparent given its broad distribution, white-tailed deer are adapted to a wide variety of habitats from heavily forested slopes to open, semi-arid plains. The increasing habitat disturbance from agriculture and logging has increased white-tailed deer populations. White-tailed deer prefer the 2nd growth forests that occur with timber harvest and rely heavily on browse that predominates under such conditions. Extensive use of riparian bottomlands and hardwood forests occurs throughout Montana; ponderosa pine habitats of the east also are used extensively. White-tailed deer spend a greater amount of time foraging than they do in any other activity. They are primarily crepuscular, moving from the cover of riparian forests to feed in adjacent open habitats during early morning and evening hours sometimes foraging into the night. In western Montana, during periods of harsh winter, Douglas fir, chokecherry, service berry, and Rocky Mountain maple contribute up to 50% of the overall food intake. Forbs and grasses account for the remaining 50% (Hildebrand 1971; Slott 1980). When snow levels are not significant, more forbs and grasses are eaten, and plants such as Oregon grape become important (Hildebrand 1971). Browse, such as pachistima, numerous forbs, and grasses are more important in spring, with forb use predominating as green-up occurs (Hildebrand 1971). In central and eastern Montana, browse such as poplar, plains cottonwood, ponderosa pine, snowberry, and chokecherry are used extensively where available, as are forbs and grasses (Allen 1968). Here, cultivated crops are also important; particularly alfalfa in summer and cereal grains such as wheat, barley, and sugar beets in autumn and winter (Dusek et al. 1989).

In eastern Montana, white-tailed deer do not migrate, although they may exhibit individual, unique patterns of habitat use in relation to resource distribution (Dusek et al. 1989). Relative home range sizes ranged from 0.65–0.72 km for females although larger home ranges occur (Dusek et al. 1989; Wood et al. 1989). Values for males approximate 1.04 km. During mild winters, white-tailed deer in the western mountains may remain on the same area year-round. Home range estimates here vary from 50–140 ha due to local habitat quality and diversity (Berner 1985; Secord 1994). If heavy snowfalls occur, animals may migrate to lower elevations or to areas where snow accumulations are naturally less.

A distinct social structure exists in which adult females and their offspring (including yearling females) associate, while adult males and often yearling males form independent fraternal groups. As the breeding season approaches, and the rut begins, male groups break up and individuals either remain solitary or begin to associate with estrous females. An elaborate array of behaviors are employed to establish dominance rankings, particularly during the breeding season. Males will mark areas by urinating and scraping the ground, or by rubbing sudoriferous secretions from forehead glands and oil secretions from preorbital and metatarsal glands on to vegetation. Pheromones at these scrapes and rub sites communicate information on social ranking to other males and also each male's reproductive condition to females. These chemical signposts may also induce and synchronize estrus in females (Sawyer et al. 1993). Most often these signals allow males to avoid direct confrontations with one another, but

fights do occur. Females also scent mark. Urinary components rubbed on the tarsal glands adhere to the sebum secreted (Sawyer et al. 1993).

When white-tailed deer feel threatened, they stomp their feet, snort, and wheeze, to startle intruders and to alert other deer. Startle behavior is followed by a flight response during which the large tail is flagged.

White-tailed deer are important as game animals and management efforts have focused on maximizing population size. Deer populations respond quickly to an increase in habitat, as occurs with extensive logging, or an increase in overall food availability, after a mild winter. Exponential rates of growth are possible, and white-tailed deer can become a nuisance around developed towns and even a serious problem in croplands. Many towns have, or are considering, hunting within city limits to control such populations.

Reproduction: Breeding begins in late autumn with conception between mid-November and mid-to-late December (Dusek et al. 1989; Slott 1980). Spermatogenesis in males begins in September, but the peak in sexual activity (the rut) is not usually until November. A female's 1st ovulation in the fall may not be accompanied by estrous behavior. A behavioral estrus lasting 24–48 hours occurs 12–13 days later at which time mating occurs. If a female does not conceive she will come into estrus at 21–30 day intervals, 2 or more times before entering an anestrous (non-breeding) condition which lasts until the following autumn.

Pregnancy lasts 187–222 days. Twinning is common and triplets may occur. Litter size and survival are influenced by habitat quality. Young are weaned by 10 months. Although females may reach sexual maturity as fawns by 6–7 months, they usually do not mate until 1.5 years. Males may also attain sexual maturity as fawns but more commonly they are 1.5 years of age at 1st breeding.

Status: Common; classified as a game species with nearly 60,000 harvested in 1995.

Smith, W. P. 1991. *Odocoileus virginianus.* Mammalian Species 388:1–13.

Extirpation, Reintroduction, and Potential Occurrence of Selected Species

Montana has been home to a wide diversity of mammals now numbering 108 species. Historically many species lived in such great abundance that they attracted the attention of naturalists and trappers. Mink, beaver, and muskrat brought a legion of trappers to the state as did bison, but these species and others suffered from such intense interest. Over the past 50 years efforts have been made to more tightly regulate the harvest of game and furbearer species and to reintroduce many which have been extirpated. In 1941, the Montana Legislature enacted laws which assured that revenue from hunting licenses would be committed to wildlife restoration and further provided legislation which gave the Fish and Game Commission authority to regulate all hunting seasons. With this revenue and the authority to manage wildlife species, a new chapter began in Montana. Mink, beaver, muskrat, river otter, and marten, although never lost from the state, were severely reduced in many regions but with tight harvest regulations and closure of trapping seasons along with reintroduction efforts they have reestablished strong populations. Some species such as the fisher and swift fox were extirpated from the state altogether due to intense trapping. The most recent record of the fisher in the state was the late 1920s and the last record of the swift fox was in 1918. Reintroduction of fisher, funded by the Montana Department of Fish, Wildlife and Parks, began in 1959 with the release of 36 animals from British Columbia into the Swan and Bitterroot mountains. Additional transplantations followed between 1988 and 1989 with the release of 110 fishers from Wisconsin and Minnesota into the Cabinet Mountains along the northwestern border of the state. These reintroduction efforts had limited success. Heavy predation of transplanted animals and natural snow conditions in many regions which make it difficult for animals to forage have limited population growth. In fact fisher probably were never abundant in Montana.

The swift fox is making a return to the state in large part due to the reintroduction efforts of the Canadian Wildlife Service. The swift fox is currently protected in Montana.

The way many species have been viewed by the general public and state agencies has changed sporadically during this century. In the late 1870s fur records indicate that over 30,000 wolf pelts were processed out of Fort Benton annually (Mussehl and Howell 1971) while today considerable money and effort is being expended to reestablish this species in Montana, Wyoming, and Idaho. Between 1942 and 1966 lynx, red fox, and raccoon were classified as predators and their harvest was uncontrolled (Mussehl and Howell 1971). Even the black-footed ferret was classified as a predator until the late 1950s. By this time no populations were known in the state and the pendulum swung toward efforts to save the species. Currently lynx, red fox, and fisher among others are identified as furbearers and their harvest is tightly regulated. The raccoon is listed as a nongame species and can still be trapped without regulation although low pelt prices seem to limit their harvest. The pendulum continues to swing. A bounty existed on mountain lions until 1962; today lion populations are rising to such an extent that suggestions are being made to allow hunting within the limits of many of Montana's cities.

Big game species have been intensively managed in the state over the past 50 years, primarily for economic reasons. Montana is 1 of the premier big game states, annually attracting tens of thousands of out-of-state hunters. Transplantations of white-tailed and mule deer, elk, sheep, goats, and prong-

horn have been made and, for many species, continue today (Mussehl and Howell 1971). Coincident with such transplantations, although, are extensive efforts to provide quality habitat. If efforts continue the uncontrolled decimation of species common in the 1800s may not be repeated.

Besides the 108 species known to live in Montana, several additional species live so close to Montana as to be nearly residents. In 1968 Hoffmann and Pattie identified 12 species that occurred in states or provinces adjacent to Montana. Since this time 5 of these, Keen's myotis (*Myotis keenii*), the pallid bat (*Antrozous pallidus*), the red bat (*Lasiurus borealis*), the hispid pocket mouse (now *Chaetodipus hispidus*), and the Arctic shrew (*Sorex arcticus*) have been found and are discussed in earlier chapters. The remaining 7 still have not been recorded in Montana although they live in close proximity to the border. In this list are 1 shrew, 4 rodents, and 2 carnivores. Additionally, the caribou used to live in the northwestern region of the state. The regional distributions of these 8 species are briefly described here in order to stimulate additional attempts to locate Montana populations.

Northern short-tailed shrew (*Blarina brevicauda*): This large shrew (up to 24 g) has been collected from Regina, Saskatchewan 152 km north of the Montana border and Fort Berthold, North Dakota, about 96 km east in the northeastern portion of the state. This shrew may live in moist grassland and riverine deciduous habitats in the extreme northeastern corner of the state. It could be readily identified since, as the name implies, this species has a short tail.

Woodchuck (*Marmota monax*): The woodchuck is closely related to the yellow-bellied and the hoary marmots found in Montana. The distribution of the woodchuck is somewhat unusual because it extends across North Dakota and curves around Montana on the north through Saskatchewan, Alberta, and British Columbia dipping back into the continental United States through the Idaho panhandle. A single specimen was collected in 1895 on Thompson Pass on the Idaho–Montana border but extensive attempts by Dr. Philip L. Wright (pers. comm.) to locate populations in Montana were unsuccessful. If present, the woodchuck would inhabit forest meadows and edges where grass is abundant. Its body color of dark brownish–reddish may be confused with that of the yellow-bellied marmot, although it lacks white between its eyes.

Plains harvest mouse (*Reithrodontomys montanus*): The plains pocket mouse is found outside the southeastern corner of Montana in both Wyoming and South Dakota. The plains pocket mouse is associated with open grassy areas from native prairie to grazed grasslands. It is similar to the western harvest mouse with which it might be confused.

Franklin's ground squirrel (*Spermophilus franklinii*): Franklin's ground squirrel lives close to the northeastern corner of the state. It has been collected near Oxbow, Saskatchewan about 128 km to the northeast. Franklin's ground squirrel prefers tallgrass prairie habitats and will move into irrigated agricultural lands. The only ground squirrel in Montana with which this species, if it occurred, would be sympatric is Richardson's ground squirrel. These 2 species can be distinguished by the former's larger size and longer, bushy tail.

Great Basin ground squirrel (*Spermophilus mollis*): Great Basin ground squirrel occurs about 48 km south of the Montana border, southwest of Dillon along Birch Creek, near Kaufman, Idaho. If it exists in Beaverhead County it could be sympatric with Uinta, Columbian, and Richardson's ground squirrels. In all instances, the Great Basin ground squirrel would be smaller (hindfoot <39 mm) and lighter in color. This species prefers arid, sagebrush habitats.

Eastern spotted skunk (*Spilogale putorius*): Identified as a distinct species in 1968

separate from the western spotted skunk, the eastern spotted skunk has been collected around the southeastern corner of the state in Wyoming (near Newcastle) and South Dakota (Harding County). Populations live within 128 km of the Montana border. Habitat preferences would be as for the western species; it would be most readily distinguished from the western spotted skunk by the absence of white hairs on the tip of its black tail.

Gray fox (*Urocyon cinereoargenteus*): The gray fox lives in North and South Dakota, and Wyoming and has been recorded closest to Montana in South Dakota (Deer Ears Butte) 69 km east of the Montana border. The gray fox is readily identified by the distinctive black streak of hairs along the dorsal surface of the tail and lack of a terminal white tip as is present in the red fox. This species could easily have extended its range westward into Montana in the past 35 years.

Caribou (*Rangifer tarandus*): Caribou lived in northwestern and northcentral Montana. Sightings in the late 1800s and early-to-mid 1900s, most often along the North Fork of the Flathead River and the Yaak River, suggest that a small population may have lived here (Freddy 1974). This population likely migrated between this region, northern Idaho (the Selkirk mountains where a small population can still be found), and British Columbia. Since the 1950s only sporadic sightings have occurred in the state and a comprehensive status review by the Montana Department of Fish, Wildlife and Parks in 1986 found no evidence of a resident population. Presently, the closest caribou population lives about 40 km north of the Montana border in British Columbia.

Dental Formulae of Montana Mammals[a]

Taxon	Incisors	Canines	Premolars	Molars	Total
Order Insectivora					
Family Soricidae					
Blarina (possible[b])	1/1	5/0	1/2	3/3	32
Sorex	1/1	5/0	1/2	3/3	32
Order Chiroptera					
Family Vespertilionidae					
Antrozous	1/2	1/1	1/2	3/3	28
Corynorhinus	2/3	1/1	2/3	3/3	36
Eptesicus	2/3	1/1	1/2	3/3	32
Euderma	2/3	1/1	2/2	3/3	34
Lasionycteris	2/2	1/1	2/3	3/3	34
Lasiurus	1/3	1/1	2/2	3/3	32
Myotis	2/3	1/1	3/3	3/3	38
Order Carnivora					
Family Canidae					
Canis	3/3	1/1	4/4	2/3	42
Urocyon (possible)	3/3	1/1	4/4	2/3	42
Vulpes	3/3	1/1	4/4	2/3	42
Family Felidae					
Lynx	3/3	1/1	2/2	1/1	28
Puma	3/3	1/1	3/2	1/1	30
Family Mephitidae					
Mephitis	3/3	1/1	3/3	1/2	34
Spilogale	3/3	1/1	3/3	1/2	34
Family Mustelidae					
Lontra	3/3	1/1	4/3	1/2	36
Gulo	3/3	1/1	4/4	1/2	38
Martes	3/3	1/1	4/4	1/2	38
Mustela	3/3	1/1	3/3	1/2	34
Taxidea	3/3	1/1	3/3	1/2	34
Family Procyonidae					
Procyon	3/3	1/1	4/4	2/2	40
Family Ursidae					
Ursus	3/3	1/1	4/4	2/3	42
Order Artiodactyla					
Family Cervidae					
Cervus	0/3	1/1	3/3	3/3	34
Alces	0/3	0/1	3/3	3/3	32
Odocoileus	0/3	0/1	3/3	3/3	32
Rangifer (possible)	0/3	1/1	3/3	3/3	34
Family Antilocapridae					
Antilocapra	0/3	0/1	3/3	3/3	32

Taxon	Incisors	Canines	Premolars	Molars	Total
Family Bovidae					
Bos	0/3	0/1	3/3	3/3	32
Oreamnos	0/3	0/1	3/3	3/3	32
Ovis	0/3	0/1	3/3	3/3	32
Order Rodentia					
Family Sciuridae					
Cynomys	1/1	0/0	2/1	3/3	22
Marmota	1/1	0/0	2/1	3/3	22
Sciurus	1/1	0/0	2/1	3/3	22
Spermophilus	1/1	0/0	2/1	3/3	22
Tamias	1/1	0/0	2/1	3/3	22
Tamiasciurus	1/1	0/0	1/1	3/3	20
Glaucomys	1/1	0/0	2/1	3/3	22
Family Castoridae					
Castor	1/1	0/0	1/1	3/3	20
Family Geomyidae					
Thomomys	1/1	0/0	1/1	3/3	20
Family Heteromyidae					
Dipodomys	1/1	0/0	1/1	3/3	20
Chaetodipus	1/1	0/0	1/1	3/3	20
Perognathus	1/1	0/0	1/1	3/3	20
Family Zapodidae					
Zapus	1/1	0/0	1/0	3/3	18
Family Muridae					
Clethrionomys	1/1	0/0	0/0	3/3	16
Lemmiscus	1/1	0/0	0/0	3/3	16
Microtus	1/1	0/0	0/0	3/3	16
Ondatra	1/1	0/0	0/0	3/3	16
Phenacomys	1/1	0/0	0/0	3/3	16
Synaptomys	1/1	0/0	0/0	3/3	16
Mus	1/1	0/0	0/0	3/3	16
Rattus	1/1	0/0	0/0	3/3	16
Neotoma	1/1	0/0	0/0	3/3	16
Onychomys	1/1	0/0	0/0	3/3	16
Peromyscus	1/1	0/0	0/0	3/3	16
Reithrodontomys	1/1	0/0	0/0	3/3	16
Family Erethizontidae					
Erethizon	1/1	0/0	1/1	3/3	20
Order Lagomorpha					
Family Ochotonidae					
Ochotona	2/1	0/0	3/2	2/3	26
Family Leporidae					
Brachylagus	2/1	0/0	3/2	3/3	28
Lepus	2/1	0/0	3/2	3/3	28
Sylvilagus	2/1	0/0	3/2	3/3	28

[a] Number of teeth on 1 side of the skull; numerator = upper jaw, denominator = lower jaw.
[b] These species likely occur in Montana.

Checklist of Montana Mammals

Class Mammalia
Subclass Theria
Infraclass Eutheria

Order Insectivora—Insectivores (10)
Family Soricidae—Shrews
____ *Sorex arcticus*—Arctic Shrew
____ *Sorex cinereus*—Common or Masked Shrew
____ *Sorex haydeni*—Hayden's Shrew
____ *Sorex hoyi*—Pygmy Shrew
____ *Sorex merriami*—Merriam's Shrew
____ *Sorex monticolus*—Dusky or Montane Shrew
____ *Sorex nanus*—Dwarf Shrew
____ *Sorex palustris*—Northern Water Shrew
____ *Sorex preblei*—Preble's Shrew
____ *Sorex vagrans*—Vagrant Shrew

Order Chiroptera—Bats (15)
Family Vespertilionidae—Vespertilionid Bats
____ *Antrozous pallidus*—Pallid Bat
____ *Corynorhinus townsendii* [*Plecotus townsendii*]—Western Big-eared or Townsend's Bat
____ *Eptesicus fuscus*—Big Brown Bat
____ *Euderma maculatum*—Spotted Bat
____ *Lasionycteris noctivagans*—Silver-haired Bat
____ *Lasiurus borealis*—Red Bat
____ *Lasiurus cinereus*—Hoary Bat
____ *Myotis californicus*—California Myotis
____ *Myotis ciliolabrum*—Western Small-footed Myotis
____ *Myotis evotis*—Long-eared Myotis
____ *Myotis lucifugus*—Little Brown Myotis
____ *Myotis septentrionalis*—Northern Myotis
____ *Myotis thysanodes*—Fringed Myotis
____ *Myotis volans*—Long-legged Myotis
____ *Myotis yumanensis*—Yuma Myotis

Order Lagomorpha—Lagomorphs (8)
Family Ochotonidae—Pikas
____ *Ochotona princeps*—Pika
Family Leporidae—Hares and Rabbits
____ *Brachylagus idahoensis*—Pygmy Rabbit
____ *Lepus americanus*—Snowshoe Hare
____ *Lepus californicus*—Black-tailed Jackrabbit
____ *Lepus townsendii*—White-tailed Jackrabbit
____ *Sylvilagus audubonii*—Desert Cottontail
____ *Sylvilagus floridanus*—Eastern Cottontail
____ *Sylvilagus nuttallii*—Mountain Cottontail

Order Rodentia—Rodents (45)

Family Castoridae—Beavers
____ *Castor canadensis*—Beaver

Family Erethizontidae—New World Porcupines
____ *Erethizon dorsatum*—Porcupine

Family Geomyidae—Pocket Gophers
____ *Thomomys idahoensis*—Idaho Pocket Gopher
____ *Thomomys talpoides*—Northern Pocket Gopher

Family Heteromyidae—Heteromyids
____ *Chaetodipus hispidus*—Hispid Pocket Mouse
____ *Dipodomys ordii*—Ord's Kangaroo Rat
____ *Perognathus fasciatus*—Olive-backed Pocket Mouse
____ *Perognathus parvus*—Great Basin Pocket Mouse

Family Muridae—Murids
____ *Clethrionomys gapperi*—Southern Red-backed Vole
____ *Lemmiscus curtatus*—Sagebrush Vole
____ *Microtus longicaudus*—Long-tailed Vole
____ *Microtus montanus*—Montane Vole
____ *Microtus ochrogaster*—Prairie Vole
____ *Microtus pennsylvanicus*—Meadow Vole
____ *Microtus richardsoni*—Water Vole
____ *Phenacomys intermedius*—Heather Vole
____ *Neotoma cinerea*—Bushy-tailed Woodrat
____ *Ondatra zibethicus*—Muskrat
____ *Onychomys leucogaster*—Northern Grasshopper Mouse
____ *Peromyscus leucopus*—White-footed Mouse
____ *Peromyscus maniculatus*—Deer Mouse
____ *Reithrodontomys megalotis*—Western Harvest Mouse
____ *Mus musculus*—House Mouse
____ *Rattus norvegicus*—Norway Rat
____ *Synaptomys borealis*—Northern Bog Lemming

Family Sciuridae—Squirrels
____ *Cynomys leucurus*—White-tailed Prairie Dog
____ *Cynomys ludovicianus*—Black-tailed Prairie Dog
____ *Marmota caligata*—Hoary Marmot
____ *Marmota flaviventris*—Yellow-bellied Marmot
____ *Glaucomys sabrinus*—Northern Flying Squirrel
____ *Sciurus carolinensis*—Eastern Gray Squirrel
____ *Sciurus niger*—Eastern Fox Squirrel
____ *Tamiasciurus hudsonicus*—Red Squirrel
____ *Spermophilus armatus*—Uinta Ground Squirrel
____ *Spermophilus columbianus*—Columbian Ground Squirrel
____ *Spermophilus elegans*—Wyoming Ground Squirrel
____ *Spermophilus lateralis*—Golden-mantled Ground Squirrel
____ *Spermophilus richardsonii*—Richardson's Ground Squirrel
____ *Spermophilus tridecemlineatus*—Thirteen-lined Ground Squirrel
____ *Tamias amoenus*—Yellow-pine Chipmunk
____ *Tamias minimus*—Least Chipmunk

____ *Tamias ruficaudus*—Red-tailed Chipmunk
____ *Tamias umbrinus*—Uinta Chipmunk

Family Zapodidae—Jumping Mice
____ *Zapus hudsonius*—Meadow Jumping Mouse
____ *Zapus princeps*—Western Jumping Mouse

Order Carnivora—Carnivores (22)

Family Canidae—Canids
____ *Canis latrans*—Coyote
____ *Canis lupus*—Gray Wolf
____ *Vulpes velox*—Swift Fox
____ *Vulpes vulpes*—Red Fox

Family Felidae—Cats
____ *Puma concolor*—Mountain Lion
____ *Lynx canadensis*—Lynx
____ *Lynx rufus*—Bobcat

Family Mephitidae
____ *Mephitis mephitis*—Striped Skunk
____ *Spilogale gracilis*—Western Spotted Skunk

Family Mustelidae—Mustelids
____ *Gulo gulo*—Wolverine
____ *Lontra canadensis*—Northern River Otter
____ *Martes americana*—American Marten
____ *Martes pennanti*—Fisher
____ *Mustela erminea*—Short-tailed Weasel
____ *Mustela frenata*—Long-tailed Weasel
____ *Mustela nigripes*—Black-footed Ferret
____ *Mustela nivalis*—Least Weasel
____ *Mustela vison*—Mink
____ *Taxidea taxus*—Badger

Family Procyonidae—Procyonids
____ *Procyon lotor*—Raccoon

Family Ursidae—Bears
____ *Ursus americanus*—Black Bear
____ *Ursus arctos*—Grizzly Bear

Order Artiodactyla—Even-toed Ungulates (8)

Family Antilocapridae—Pronghorn
____ *Antilocapra americana*—Pronghorn

Family Bovidae—Bovids
____ *Bos bison*—Bison
____ *Oreamnos americanus*—Mountain Goat
____ *Ovis canadensis*—Bighorn Sheep

Family Cervidae—Cervids
____ *Alces alces*—Moose
____ *Cervus elaphus*—Wapiti or Elk
____ *Odocoileus hemionus*—Mule Deer
____ *Odocoileus virginianus*—White-tailed Deer

One hundred and eight species currently occur in Montana. Species which may occur are:

Blarina brevicauda—Short-tailed Shrew
Marmota monax—Woodchuck
Reithrodontomys montanus—Plains Harvest Mouse
Spermophilus franklinii—Franklin's Ground Squirrel
Spermophilus mollis—Great Basin (Piute) Ground Squirrel
Spilogale putorius—Eastern Spotted Skunk
Urocyon cinereoargenteus—Gray Fox
Rangifer tarandus—Caribou or Reindeer

Glossary

abiotic—not of living systems.
altricial—birth at a very immature state of development (e.g., eyes and ears closed, lack fur).
anterior—toward the head.
anestrus—the nonbreeding period of a reproductively mature female.
auditory bullae—the bony capsule surrounding the inner ear.
brachyodont—molariform teeth with a low crown that ends at the gum line and has distinct roots.
broken patterning—a form of protective coloration in which the shape and size of the animal is obscured because of stripe or spotting patterns.
bunodont—a tooth cusp pattern characterized by rounded surfaces and a complete covering of enamel; specialized for crushing food.
calcar—cartilaginous projection from the ankle and serves to support the pterygium in bats.
canine—1 of 4 major types of teeth; specialized for grasping, puncturing, and tearing meat.
carnassial (sectorial)—specialized molariform teeth (specifically the last upper premolar and 1st lower molar) modified with a sharp cusp surface for shearing of food.
carnivore—an animal that eats predominantly animal materials.
commensal—an animal or plant that lives with another for support.
coprophagy—ingestion of specialized feces for absorption of additional nutrients; exhibited primarily by lagomorphs.
counter shading—a form of protective coloration where the dorsal (top) surface of the mammal is darker than the ventral (bottom) surface.
crepuscular—during early morning and evening.
delayed implantation—arrested embryonic development prior to attachment of the embryo to the uterine lining (endometrium).
delayed fertilization—a lengthy delay between copulation and conception involving storage of sperm in the female's reproductive tract.
delayed development—very slow embryonic growth and development after attachment of the embryo to the uterus.
diastema—a gap between incisors and premolars best exhibited in rodents and lagomorphs.
digitigrade—form of locomotion where walking occurs on the digits.
diurnal—during the daytime.
dorsal—top surface (along the back of an animal or top of skull).
echolocation—process whereby objects can be located based upon comparison of emitted sound waves and the received echo of these sound waves.
estrous cycle—a type of reproductive cycle in which sexual response occurs only during the mid-cycle estrus.
estrus—the behavioral state associated with a female's willingness to mate.
eutherian—a mammal with an elaborate placenta for nutrient and waste exchange between mother and fetus.
ever-growing teeth—teeth that continually grow from their base throughout the animal's life.
fenestrated—perforated.
foramen (pl. foramina)—an opening.
fossorial—an animal that burrows underground to live.
gram—unit of mass equal to 0.035 ounce or 0.002 pound.
guard hair—1 of 2 types of hair; longer and less numerous than underfur primarily used for protection of undercoat.
hectare (ha)—unit of area equal to 2.471 acres (10,000 m^2).
herbivore—an animal that eats predominantly plant materials.

hertz [Hz]—a unit of frequency equal to 1 cycle/second of a sound-wave pattern.
heterodont—dental pattern in which >1 type (shape) of tooth exists.
heterothermy—variable body temperature
hibernation—physiological state where a mammal lowers its body temperature significantly, approaching ambient temperature; heart rate and respiratory rate are greatly reduced.
homeotherm—a "warm-blooded" animal; constant body temperature.
homodont—a dental pattern where all teeth are the same shape.
hypsodont—molariform teeth possessing a high crown that extends nearly to the base of the mandible with no distinct appearance of roots.
in utero—within the uterus.
incisor—1 of 4 major types of teeth; anterior teeth used primarily for nipping.
induced ovulation—ovulation in response to mating.
interfemoral membrane (pterygium)—membrane supported between the femurs.
keel—bony spur off of calcar of ankle in bats which supports pterygium or process along the sternum.
kilogram—unit of mass equal to 1,000 g (2.20 pounds).
kilohertz [kHz]—a unit of frequency equaling 1 thousand cycles/second of a sound wave pattern (1,000 hertz).
lateral—toward the side.
lophodont—a tooth cusp pattern characterized by surfaces that are incompletely covered by enamel, interspersed with dentine, and in which the layering runs in a transverse direction with respect to the jaw.
medial—along the mid-line of the body.
mesic—moist or wet.
metatherian—"pouched" mammals; females possess a ventral pouch in which young are nursed.
molar—1 of 4 major types of teeth; primarily used for crushing food; generally larger than premolar teeth with more complex roots and cusps.
monestrous—1 breeding cycle (estrous cycle)/breeding period.
mycophagist—an animal that eats fungi.
nasal septum—partition between nasal bones.
nocturnal—during the nighttime.
obligate delay—a delay which occurs regardless of the physiological state of the animal.
omnivore—an animal that eats plant and animal materials and is thus a generalist.
parturition—birth.
philopatry—offspring remain in parental territories.
plantigrade—form of locomotion where walking occurs on the soles of the feet.
polyestrous—a condition in which females may return to estrus repeatedly within a breeding season.
precocial—birth in a very mature condition (e.g., eyes and ears open, furred).
premolar—1 of 4 major types of teeth; primarily used for crushing food (however see "sectorial"); generally smaller than molar teeth and with less complex roots and cusps; located in front of molars and behind canines.
prismatic—prism shaped (series of angles).
pterygium—membrane supported by hindlegs and encompassing the tail in bats.
recrudescence—renewal of tissue activity.
rostrum—nasal region of skull.
sectorial (carnassial)—specialized molariform teeth (specifically the last upper premolar and 1st lower molar) modified with sharp cusp surfaces for shearing of food.
selenodont—a tooth cusp pattern characterized by surfaces that are incompletely covered by enamel, interspersed with dentine, and in which the layering runs lengthwise to the jaw.
spontaneous ovulation—shedding of an egg (ovulation) without external stimulation.
torpor—physiological state where a mammal reduces its body temperature to save energy; heart rate and respiratory rate are concomitantly reduced; physiological parameters are not as greatly altered as during hibernation.

transverse—across.
underfur—1 of 2 types of hair; more numerous and softer than guard hairs primarily used for insulation.
unguligrade—form of locomotion where walking occurs on the tips of the digits.
unicuspid—single-cusped teeth found in insectivorous (shrews); their developmental history is unclear.
ventral (venter)—bottom surface (along the belly of an animal or underside of skull).
vibrissae—a type of specialized hair associated with tactile sensations.
xeric—arid.

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1 centimeter (cm) = 0.39 inches; 2.54 cm/inch

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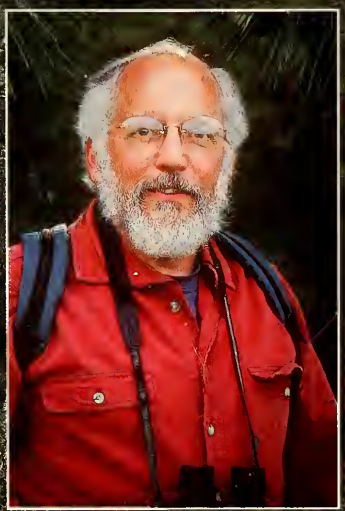

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